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COMPARISON OF THE BEHAVIOR OF STOCK AND INBRED ALBINO RATS

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For a number of years the Wistar Institute of Anatomy and Biology has been carrying on experiments in inbreeding the albino rat, *Mus Norvegicus albinus*, for the purpose of studying the anatomical effects of such procedure. In October, 1911, some of the rats, which had then been inbred to the sixth generation, were sent to the Johns Hopkins University and were used by Doctor Basset[1] for comparative studies in habit formation.

In April, 1913, while Basset's experiments were still in progress, the suggestion of similar coöperation in the study of the effects of inbreeding on the formation of habits was made by the Wistar Institute to the Harvard Psychological Laboratory and gladly accepted. It was then so late in the collegiate year that only a few preliminary experiments were made at that time by Professor Yerkes and two students, using the method of brightness discrimination. The following October the writer undertook, at Professor Yerkes' suggestion,[2] a study of certain forms of behavior of these rats, which had then reached the twelfth generation of inbreeding. The scope of the work was more limited than that of Doctor Basset because of lack of time, and the number of animals tested was smaller. My thanks are due Doctor Donaldson of the Wistar Institute for supplying us with our original stock of rats, and to Doctor Hatai for the examinations which supplied the anatomical data. I wish, also, to express my thanks to Mr. Pedrick and Mr. Dine for assistance with some of the experiments.

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[1] Basset, G. C. Habit formation in a strain of albino rats of less than normal brain weight. *Behavior Monographs*, 1914, vol. 2, no. 4.

[2] In suggesting to Mrs. Yerkes a comparative study of stock and inbred rats, I expressed especial interest in the attempt to analyze "the temperament" of the animals, for certain previous observations in comparison with those reported by Basset had convinced me that crude measurements of modifiability, if directly compared, might lead to seriously misleading conclusions because of differences in timidity, savageness, aggressiveness, sensibility, etc., in the two groups of organisms under observation.

Mrs. Yerkes' work, unfortunately, was seriously interfered with by unexpected difficulties in the breeding of rats in the new Harvard Laboratory of Animal Psychology. From the statistical standpoint, her results are unsatisfactory because of this difficulty.

The inbred rats which were sent to us in October, 1913, were of the thirteenth generation. In January some belonging to the twelfth and also to the fourteenth generation were obtained. Our normal control rats were secured partly from the Wistar Institute and partly from Miss Lathrop, Granby, Massachusetts. They were kept in a special room in the laboratory on the fourth floor of Emerson Hall, in clean wire cages, with sawdust on the floor and shredded tissue paper for nests. They were fed bread soaked in milk, cracked corn, oats, and occasionally green stuff, such as lettuce and celery tops. For some reason still unknown to us, although they appeared for the most part to be in excellent physical condition, they bred very slowly, and the work was occasionally delayed for lack of material of the right age. The rats with which the later experiments were made were also considerably underweight for their age, as shown in the anatomical data of table 11 (p. 293). It was found impracticable to forward to Philadelphia for examination the rats used in the earlier tests, so that the relative brain weights are given for only the last lot of seven rats.

Two methods were employed in the comparative study of the behavior of stock and inbred animals: the maze and the brightness discrimination methods. Time, distance, and error data were obtained for the maze experiments; and time and error data for the discrimination experiments.

1. MAZE EXPERIMENTS

The type of maze used in these experiments was the circular one devised by Watson.[3] The method of recording the path was that described by Yerkes and Kellogg.[4] A similar method has also been used by Miss Hubbert.[5]

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[3] Watson, J. B. A circular maze with camera lucida attachment. *Jour. An. Behavior*, 1914, **4**, 56-59.

In our work the path through the maze was somewhat modified from that used by Miss Hubbert, as indicated in the accompanying figure 1. Instead of turning alternately to the right and then to the left as in the Johns Hopkins maze, in our maze a rat must turn R, L, R, R, L, L, R in order to traverse the maze correctly. This may have increased the difficultness.

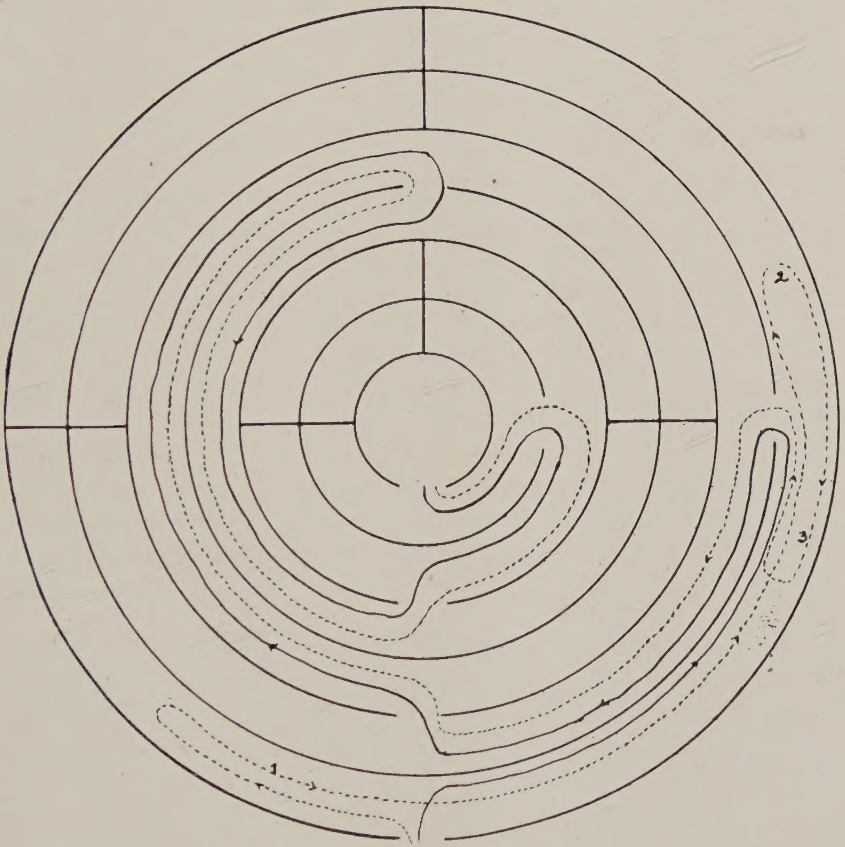

FIGURE 1.—Maze. ——— Direct path; ...... Path with three errors.

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[4] Yerkes, R. M. and Kellogg, C. E. A graphic method of recording maze-reactions. *Jour. An. Behavior*, 1914, **4**, 50-55.

[5] Hubbert, H. B. Time versus distance in learning. *Jour. An. Behavior*, 1914, **4**, 60-69.

The correct path is shown by the solid line in the figure. There are eleven blind alleys which may be entered either by going straight ahead past an opening or by turning in the wrong direction after passing through an opening. Entering any one of these alleys was counted an error; also turning back so that the animal was running in the wrong direction in any section of the maze, i.e., between successive openings, was counted an error for each section of the maze through which it ran. The dotted line in figure 1 shows a path in which three such errors occur. This definition of an error is in accordance with Mrs. Hicks' two propositions, namely, that errors shall include all total and partial returns, and that a runway, the distance between two corners, or its equivalent in the circular maze, the distance between two openings, shall be taken as the unit of error.[6]

After a number of animals had been tested in this form of maze, it was decided to simplify the maze and shorten the path to the centre by cutting out the outer circles. The inner wall of the outer circle was shifted so that the opening faced the entrance to the maze. Blocks were then placed on either side of the opening so that a straight passageway was formed from the entrance through to the third circle. The correct turns were then L, R, L, L, R. This form is hereafter referred to as the short maze. That this change made the problem much easier is shown by the fewer trials required to learn it correctly, as indicated in table 1, where the stock rats (average age about 66 days) in the long maze required an average of 55.25 trials; the inbred, 65 trials; in the short maze (age 35 days), stock, 19.2 trials; inbred, 23.75.

The attachment for recording the maze path consists, briefly, of a mirror attached to the ceiling; this mirror reflects the image of the maze through a lens to a drawing board, enveloped in a hood of black cloth, and holding a pad of paper on each sheet of which had been printed a diagram of the maze. This diagram exactly fitted the image of the maze received from the lens. The sheets of paper could be easily and quickly removed with practically no interruption of the tracing and thus the course of a rat in its devious wanderings could be readily followed with a pencil on successive sheets. In early tests of a rat frequently seven or eight sheets would be used for one record. The record thus obtained was traced with a Keuffel and Esser chartometer, and the result was a record of the distance, in centimeters, of the path as projected on the paper. The ratio of the size of the image to that of the maze was as 1 to 6.75. The number of centimeters as recorded by the chartometer was therefore multiplied by 6.75 to obtain the actual distance covered by the rat. The distance is given in centimeters in the accompanying tables.

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[6] Hicks, V. C. The relative values of different curves of learning. *Jour. An. Behavior*, 1911, 1, 138-156.

In preliminary experiments, in order to remove possible error due to fear of the strange environment, all blocks shutting off the blind alleys were removed and the animals allowed to roam at will throughout the maze, finding their way to the food in the center if possible. One such trial a day was given for three, or five, days prior to the regular experiments. Later, the better expedient was adopted of feeding the animals in the food box in the centre of the maze for twenty minutes each day for three to five days. When the regular experiments were begun with the long form of maze the rats were allowed to feed in the centre for five minutes after completing the circuit and were then given additional food in the cage. In the short form of maze the animals were fed only in the food-box for twenty minutes at the close of the day's work. By the latter method it was possible to regulate better the amount of hunger which served as an incitement to activity in traversing the maze, but it is possible that with only one such trial a day the animals were underfed. This may account for their small size, as noted later.

The habit was considered perfect when a rat made three correct runs in succession, i.e., runs in which there were no errors. The distance for the shortest path in the long maze was 556.88 centimeters; in the short maze, 357.75 centimeters.

In the preliminary experiments a rat was allowed thirty minutes in which to find the way into the centre. Later this was reduced to fifteen minutes, since it was discovered that almost invariably, if the rat had not succeeded within the first fifteen minutes, it spent the remainder of the time sitting still in a corner or doorway. The figures followed by a + in the time columns of the tables indicate that a rat was given the full allowance of time and then removed for the day. When

TABLE 1

Stock	Inbred	Gen.	Age	P. T.	Maze	No. of Tr.	Av. No. of Tr.	M. No. of Tr.	Abs. Ret.
23♂	.....	.....	70d.	Open M.	Long	67	Stock	29	60″
47	.....	.....	51	Fed	"	35	.....	6	87.1
22♀	.....	.....	?	Open	"	98	55.25	6+	67
50	.....	.....	71	"	"	41	.....	9+	58
.....	1♂	13B	69	"	"	80	Inbred	32	83.3
.....	2♀	13B	74	"	"	68	65.00	12+	79.3
.....	62	13A	55	"	"	47	.....	.....	.....
81♂	.....	.....	36	Fed	Short	18	Stock	.....	.....
83	.....	.....	35	"	"	32	.....	.....	.....
85	.....	.....	41	"	"	12	19.2	.....	.....
80♀	.....	.....	35	"	"	16	.....	.....	.....
82	.....	.....	36	"	"	18	.....	.....	.....
.....	87♂	13A	37	"	"	23	Inbred	.....	.....
.....	89	13A	37	"	"	20	23.75	.....	.....
.....	84♀	13A	37	"	"	26	.....	.....	.....
.....	86	13A	37	"	"	26	.....	.....	.....

the tendency merely to sit still without effort to solve the problem was very marked, the animal was given a chance on at least three successive days, and showing no improvement, was discarded. Fifteen rats, seven stock and eight inbred, were discarded on this basis. Sixteen rats completed the training, nine stock and seven inbred, and a seventeenth (stock) whose timidity and wildness had made her exceptional throughout the experiments, was discarded after the one hundred and tenth trial, as she showed little sign of improvement.

The rats with which the first tests were made were eight to ten weeks old. The later ones were younger, for the effort was made to start them at seven weeks (later at five weeks). The nine rats used in the short maze were all born on the same day and were thirty-five days old when the experiments were begun. Not all were started on the same day.

In table 1 is presented a list of the rats used in the maze experiments, their sex, strain, generation, age, preliminary training, number of trials required for learning the maze and for re-learning after an interval of twenty-eight days, and the

TABLE 2

DATA FOR STOCK RATS IN LONG MAZE

Females				Males			
No.	Time*	Error	Dist.	No.	Time	Error	Dist.
1	1118.5	31.0	3584.3	1	1313.7	32.5	5158.7
6	142.2	11.0	1576.1	6	199.6	13.5	2386.1
11	65.1	4.5	968.6	11	663.0	10.0	1476.6
16	38.3	3.0	528.2	16	74.2	4.5	985.5
21	64.3	6.0	894.5	21	144.0	7.0	1623.4
26	47.0	3.5	1161.0	26	103.7	5.5	1201.6
31	37.5	3.5	666.5	31	86.4	2.0	865.7
36	68.2	9.0	1216.7	36	27.0	2.0	877.5
41	34.6	3.0	793.1	41	12.2	0.0	580.5
46	23.0	2.0	644.6	46	58.2	6.0	1485.0
51	27.0	4.0	1134.0	51	31.0	5.0	1377.0
56	31.4	1.0	681.8	56	55.5	9.0	2217.4
61	35.2	2.0	880.9	61	13.5	1.0	648.0
66	64.7	3.0	756.0	66	12.8	0.0	556.9
71	16.0	1.0	658.1	67	7.3	0.0	540.0
76	22.0	1.0	658.1	68	12.0	0.0	536.6
81	116.4	12.0	2322.0				
86	53.6	2.0	796.5				
91	35.0	1.0	742.5				
96	20.2	0.0	543.4				
97	15.0	0.0	553.5				
98	29.4	0.0	550.1				

* Time in seconds.
Distance in millimeters.

TABLE 3

DATA FOR INBRED RATS IN LONG MAZE

Females				Males			
No.	Time	Error	Dist.	No.	Time	Error	Dist.
1	991.6	12.0	2246.1	1	135.8	5.0	1269.0
6	281.6	8.5	1954.2	6	86.5	5.0	1285.9
11	150.3	5.0	1270.7	11	127.2	12.0	2062.1
16	352.0	10.0	2543.1	16	29.0	2.0	887.6
21	146.0	6.5	1550.8	21	52.0	9.0	1687.5
26	314.3	7.0	1706.0	26	92.0	8.0	1431.0
31	129.6	3.0	943.3	31	87.2	2.0	897.8
36	73.1	3.0	1017.5	36	61.2	2.0	624.4
41	61.6	2.0	799.9	41	160.3	6.0	1552.5
46	26.0	0.0	577.1	46	166.0	5.0	1531.0
51	92.8	4.0	1312.9	51	53.0	2.0	803.3
56	157.0	1.0	708.8	56	63.6	2.0	891.0
61	70.6	1.0	661.5	61	55.2	3.0	705.4
66	12.5	0.0	560.3	66	61.6	2.0	830.3
67	10.5	0.0	550.1	71	126.1	5.0	1296.0
68	11.0	0.0	556.9	76	16.0	0.0	594.0
				80	9.4	0.0	563.6

TABLE 4

DATA FOR STOCK AND INBRED RATS IN SHORT MAZE

5 Stock				4 Inbred			
No.	Time	Error	Dist.	No.	Time	Error	Dist.
1	373.4	16.0	1998.8	1	900.0+	10.0	664.9
2	125.7	9.4	1128.6	2	765.0	18.5	1515.4
3	149.5	8.0	1208.2	3	639.3	17.2	1532.2
4	61.7	6.8	905.8	4	416.5	11.5	1292.6
5	61.9	7.4	1200.8	5	313.2	6.0	836.1
6	35.5	5.0	913.3	6	70.4	5.7	799.8
7	41.1	7.0	988.9	7	50.4	5.0	744.2
8	24.3	3.4	719.5	8	63.7	8.5	1354.2
9	24.6	3.4	724.3	9	27.5	4.7	816.7
10	15.5	2.2	587.9	10	29.4	5.5	958.5
11	9.0	0.8	428.6	11	33.7	5.5	1151.7
12	7.9	0.6	422.5	12	44.8	7.0	1178.7
13	10.4	1.2	540.8	13	42.6	6.2	1326.4
14	10.2	1.0	471.6	14	27.2	4.0	897.7
15	8.7	1.2	475.0	15	43.6	7.5	1180.0
16	10.6	1.5	552.6	16	29.2	4.0	798.2
17	8.1	0.6	462.4	17	15.9	5.7	1106.1
18	11.9	1.6	578.2	18	15.6	2.7	615.1
				19	21.3	2.5	800.7
19	25.9	3.0	749.3	20	20.8	1.2	551.8
20	4.9	0.0	357.8	21	37.4	3.0	803.2
21	14.1	1.0	681.8	22	22.1	1.6	535.5
22	15.0	0.0	367.9	23	11.0	0.6	486.0
23	17.1	0.0	378.0	24	10.1	0.0	383.1
24	12.3	2.0	587.3	25	7.2	0.0	379.7
25	23.2	2.0	756.0	26	7.6	0.0	376.3
26	17.2	0.0	398.3				
27	8.0	0.0	381.4				
28	16.2	2.0	735.8				
29	27.2	2.0	779.6				
30	8.4	0.0	378.0				
31	12.0	0.0	381.4				
32	19.2	0.0	374.6				

"absolute retention," i.e., the length of time required for the first trial after that interval.

In table 2 are given the averages of records of time, errors, and distance for four stock rats, two males and two females, trained in the long maze; in table 3 are the records for three inbred rats, also in the long maze;[7] in table 4 the records for five stock rats (three males and two females) and four inbred rats (two males and two females) trained in the short maze.

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[7] In tables 2 and 3 only the records for every fifth trial are here given in order to save space. The records given in table 4 are complete, however, and the curves plotted from these records only are shown.

Figures 2, 3 and 4 give, respectively, time, distance, and error records for males and females averaged together, in the short maze.

Consulting the tables for the males in the long maze, we find that during the first thirty trials, time, distance, and error records of the stock rats were higher than for the inbred; that there were more high records for the stock than for the inbred rats in all three items, especially time; and further, that the stock rats acquired the habit sooner than the inbred (table 1), the former requiring an average of fifty-one trials, the latter, eighty. In other words, the male stock rats in the long maze traveled greater distances, took a longer time for most of the trials, especially the first twenty, and made on the whole more errors, but acquired a perfect habit sooner than the inbred.

The same thing does not appear to be true of the females. Here the course of the inbred females is much more erratic than that of the stock. The stock rats, because of persistent activity,

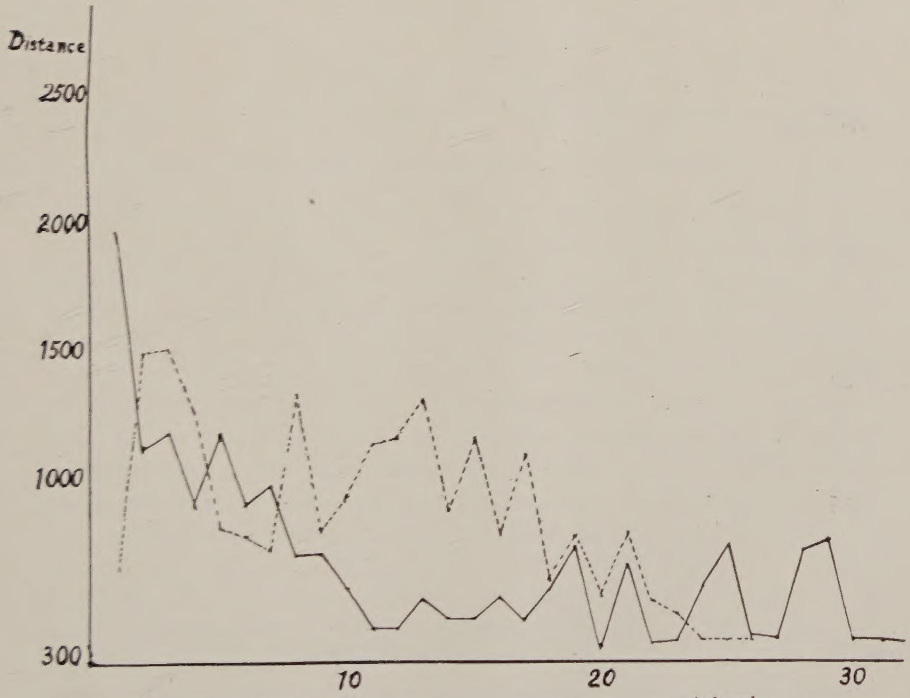

FIGURE 2.—Short maze. Distance in mm. Stock, ——— ; inbred........

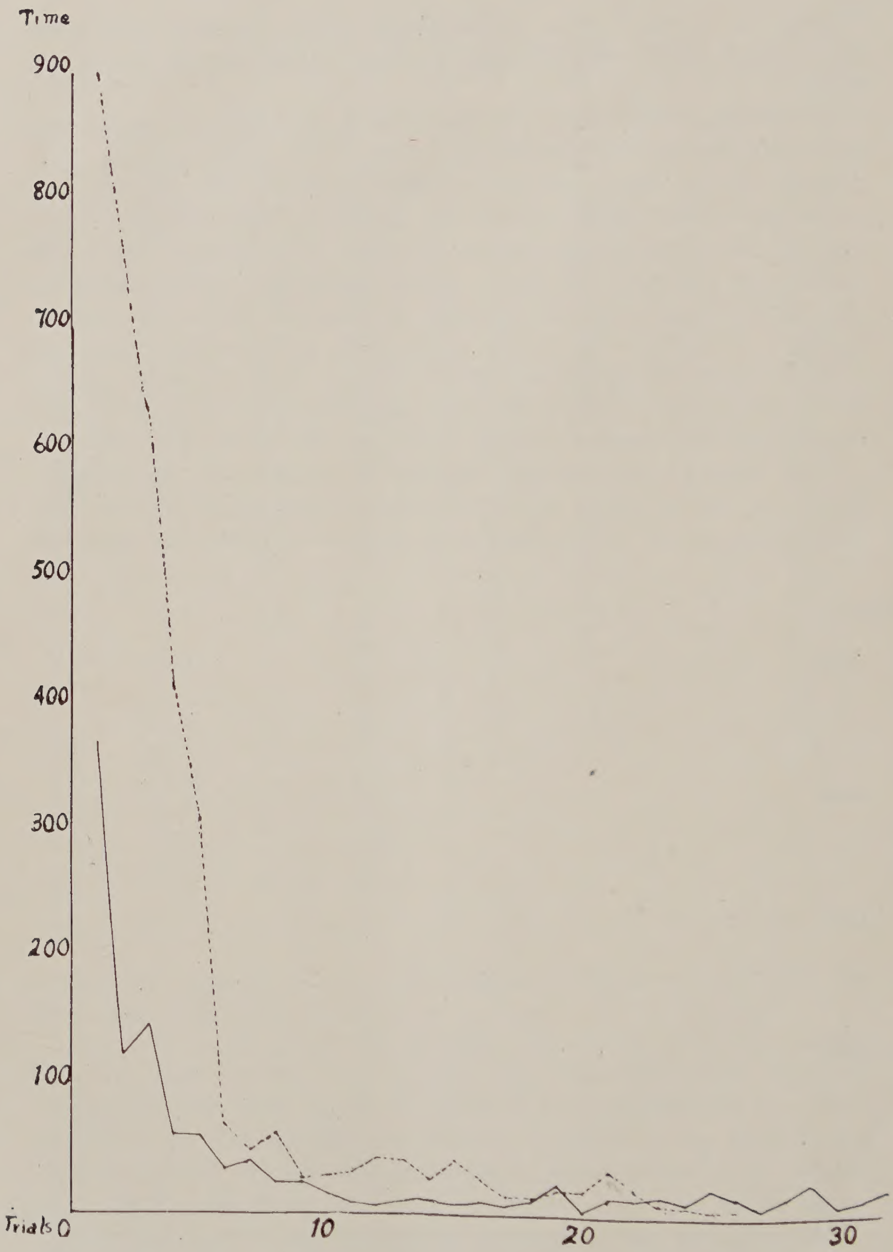

FIGURE 3.—Short maze. Time in seconds. Stock, ——— ; inbred, ...

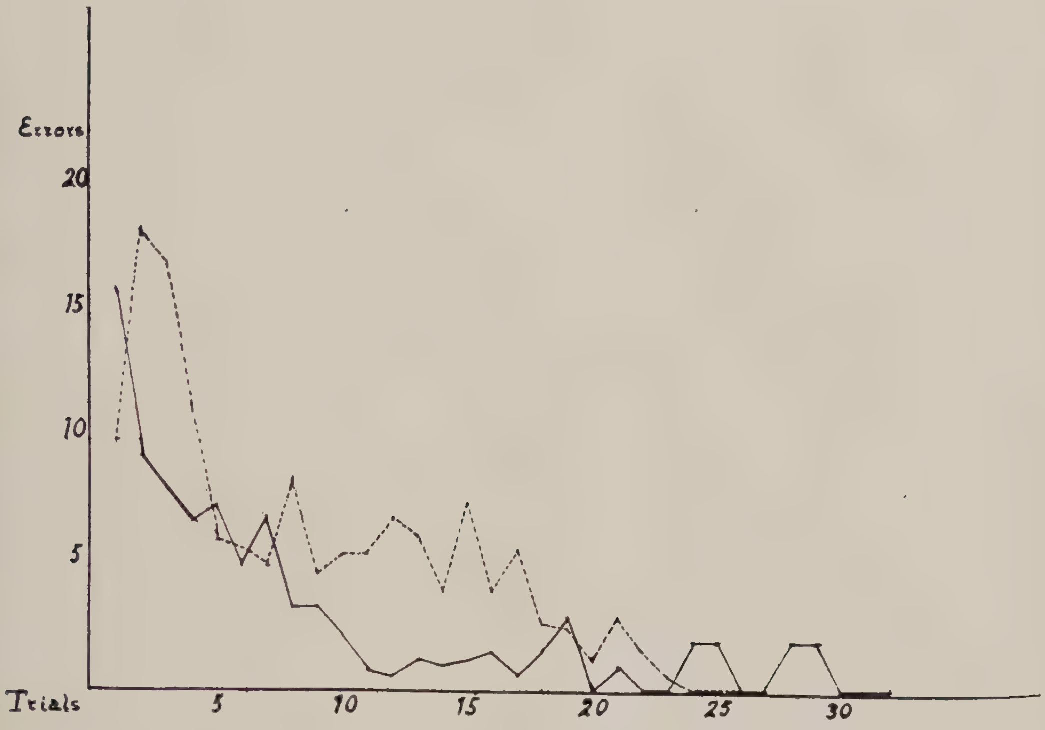

FIGURE 4.—Short maze. Errors. Stock, ——— ; inbred, ...

required more than the allotted limit of fifteen minutes in order to complete the first trial. The time, however, immediately and rapidly decreased and remained low and fairly regular. The inbred rats, on the other hand, spent the full time allowed in the first two trials sitting in corners, and did not reach the centre at all. The distance and error records were therefore very low at the beginning, but increased as activity increased. The amount of time correspondingly increased, but in much greater degree and with great irregularity. The curves which were plotted for these records but are not reproduced show for the inbred rats sharp variations from day to day in time required for each trial between the tenth and thirtieth trials and high records obtained. After the thirtieth trial the time was only a little greater, while distance and error records for the inbred rats were on the whole lower than those for the stock rats. The inbred females also acquired a perfect habit sooner, with an average of 57.5 trials as against 69.5 trials for the stock females.

Consulting the time, distance and error curves for the short maze (figures 2-4) we find the time records very high for the inbred rats during the first five trials. In the first trial, in fact, none of them finished the trip in the time allowed (900″) and one did not even in the third trial. Evidently because of timidity they sat still most of the time allowed, making a low distance record for those trials. As they became accustomed to the maze the time rapidly diminished, though remaining a little higher than the stock records until the last few trials. The distance, and correspondingly the error records, on the other hand, increased after the first and are considerably higher than for the stock rats. The inbred rats, therefore, apparently traveled at a higher rate of speed when their timidity was once overcome. The distance and error records for the inbred rats also show greater irregularity from day to day.

In both long and short mazes, the distance and error curves for each set of rats are very similar, almost identical. Where differences occur they may be due to the place where the error occurs, i.e., in the long outer runways or the inner and shorter ones. It will be noticed, however, that the disparity between time and distance curves is very great, especially in the early trials.

In a discussion of the relative values of the different curves of learning, Mrs. Hicks[8] refers to the distance curve as a nearly ideal one but impracticable because of the difficulties of recording the distance exactly. These difficulties have since been overcome. Miss Hubbert[9] in her comparisons of time and distance curves found them so similar in character "when normal animals are tested that it is impossible to state which is the better criterion of learning." In the present comparison of behavior of stock and inbred rats, the time and distance curves are not similar. If either time or distance were taken alone, a true picture of the learning process would not be obtained. The records of distance alone would make the inbred rats appear the quicker, at first, in learning the correct path, which the time records show was not the case. A combination of time and error or time and distance curves apparently gives the most adequate representation of the facts obtained from these stock and inbred rats.

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[8] Hicks, V. C. The relative values of the different curves in learning. *Jour. An. Behavior*, 1911, **1**, 138-156.

[9] Hubbert, H. B. Time versus distance in learning. *Jour. An. Behavior*, 1914, **4**, 60-69.

2. DISCRIMINATION METHOD

When the inbred rats were first received from the Wistar Institute, a few preliminary experiments were made by Professor Yerkes and two students, using the brightness discrimination method and twelve animals, six stock and six inbred, three males and three females each. The results of these experiments are given separately from the writer's, which were conducted a year later at the Franklin field-station. The former animals are designated Group 1, the latter, Group 2. The apparatus was exactly the same for all. Artificial light was used for the earlier, and daylight for the later experiments. The animals of the first group were from 46-55 days old when the experiments were begun; those of the second group were eight of the nine young rats which had recently been tested in the short maze. As soon as the maze experiments were finished the rats were sent from Cambridge to Franklin and experiments were begun June 17. The rats were at this time 75 days old. One of the stock rats met with an accident soon after the beginning of the experiments so that the results are given for four stock and four inbred rats, two males and two females each.

The apparatus used was in essentials the Yerkes discrimination box.[10] It consisted of a box 52 cm. long by 40 cm. wide by 18.5 cm. deep. Attached to this at one end was a smaller food box 16 cm. by 14 cm. by 18.5 cm., having a hinged wooden cover, with a small hole in the centre. An animal to be tested was allowed to enter from the food box, by means of a sliding door, a narrow passage. This led through a door of wire mesh, swinging inward from the top, to a chamber 15.4 cm. by 18 cm. From this led two pathways or discrimination boxes, 20 cm. by 8.5 cm., differentiated only by the amount of light entering them. These communicated by openings in the side walls at the rear with passageways by means of which return was effected to rooms adjoining the entrance passage from which the animal could reënter the food box. The floor of the discrimination boxes was covered with a series of copper wires connected with a No. 6 Columbia dry cell and a Porter inductorium set at 5.75 on the scale. Used in daylight the experiment box was placed facing a window so that when uncovered the two boxes received the same amount of light.

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[10] Yerkes, R. M. The dancing mouse. New York, 1908, p. 92.

The first degree of difference in amount of light was made when a piece of black cardboard, black side down, was placed on top of one box and the other was left open. These were designated, then, the dark, D, and the light, L, boxes. The rats were required to choose the light box; if they chose the dark one, they received a slight electric shock from the wires on the floor of the box and were not allowed to pass through. The dark side was changed from left to right irregularly but according to a definite schedule printed on blanks on which the records were kept. The time from entrance through the swinging wire door into the chamber facing the dark and light boxes until the choice was made was taken by means of a stop watch. It was called a choice when an animal placed both forefeet far enough across the wires to receive the shock, if the choice were wrong. This discrimination time varied from four-tenths seconds to more than thirty minutes when the animals were timid or discrimination was difficult. The total time required for the regular daily series of five or ten trials was also noted.

In order to teach the method of procedure and also to test possible preference for dark or light, two preliminary series, A and B, of ten trials each were given without shock and with the dark box open for free passage through. Each regular series thereafter consisted of five trials, and one series was given a day, at the same hour of the morning. One rat was in the apparatus at a time. They were not hurried but were gently and firmly directed through the entrance doors, allowed to choose, guided back, if necessary, to the food box, and allowed to eat for 15-30″ before the next trial. The readiness with which the rats learned of their own initiative to pass through the swinging wire doors was used as a measure of their degree of initiative. This is discussed in the next section. Bread crumbs soaked in milk and mixed grains were the food used in the food box. After the series for the day was completed the animals were allowed to feed for half an hour in another cage before being returned to their own cage.

TABLE 5. DISCRIMINATION EXPERIMENT. GROUP 1. MALES

No.	Stock No. 14♂				Stock No. 19♂				Stock No. 25♂				Inbred No. 30♂				Inbred No. 1♂				Inbred No. 10♂			
	Con.	R.	W.	Av. T.	Con.	R.	W.	Av. T.	Con.	R.	W.	Av. T.	Con.	R.	W.	Av. T.	Con.	R.	W.	Av. T.	Con.	R.	W.	Av. T.
A	P	4	6		P	1	2	3.0	P	5	5	1.5	P	2	8		P	6	4	2.0	P	6	4	1.4
B	P	4	6		P	6	4	1.0	P	5	5	16.8	P	1	9		P	5	5	.9	P	5	5	1.1
1	1	2	3	6.6	1	3	2	1.0	1	3	2	24.8	1	4	1	30.6	1	2	3	3.8	1	3	2	13.4
2		5	0	8.8		2	3	1.2		5	0	13.8		5	0	38.8		3	2	6.2		2	3	4.6
3		3	2	14.8		3	2	233.0		3	2	18.6		5	0	17.8		3	2	15.6		2	3	2.2
4		4	1	13.6		2	3	191.0		5	0	33.0		4	1	21.8		3	2	314.8		3	2	1.0
5		5	0	5.4						5	0	11.8		5	0	7.4		4	1	29.2		3	2	2.0
6		4	1	13.8		Sa	va	ge.		5	0	20.2		5	0	19.4		4	1	18.6		2	3	1.4
7		5	0	4.2						5	0	14.0		5	0	12.4		5	0	30.8		2	3	1.4
8		5	0	4.8		3	2	123.8						5	0	8.2		4	1	8.8		3	2	1.2
9		5	0	6.2														5	0	10.4		3	2	1.0
10		5	0	10.8		5	0	194.2										5	0	4.2		3	2	1.2
11						5	0	302.8										9	1	12.7		9	1	6.7
12						5	0	73.2										10	0	14.1		6	4	5.1
13						10	0	38.4						10	0	23.9		10	0	14.2		9	1	10.4
14														10	0	4.9		9	1	19.1		8	2	5.4
15														10	0	6.3		10	0	9.7		10	0	1.4
16										10	0	5.3										10	0	3.7
17										10	0	6.5										10	0	3.4
18	2	4	1	24.6	2	5	0	150.6	2	4	1	17.8	2	5	0	11.6	2	5	0	22.0	2	5	0	16.4
19		5	0	5.8		4	1	194.0		4	1	23.2		5	0	5.2		4	1	32.0		4	1	8.0
20		8	2	5.3						8	2	25.2		10	0	7.4						9	1	6.5
21		9	1	2.8						8	2	96.7		9	1	13.7						9	1	8.1
22		10	0	19.0						4	1	106.0		10	0	11.7						10	0	10.6
23										4	1	46.2										9	1	9.8
24	3	5	0		3	10	0	128.6	3				3	3	2	6.0	3	10	0	32.0	3	2	3	23.4
25						10	0	105.5										8	2	76.6		4	1	15.6
26	4	5	0	2.6									4	3	2	27.4								
27	6	5	5	28.0									6	9	1	16.1								
28	5	3	2	30.6									5	6	4	55.4								
29	4	10	0	17.1									4	6	4	27.9								

TABLE 6. DISCRIMINATION EXPERIMENT. GROUP 1. FEMALES

No.	Stock No. 13 ♀				Stock No. 21 ♀				Stock No. 24 ♀				Inbred No. 80 ♀				Inbred No. 90 ♀				Inbred No. 20 ♀			
	Con.	R.	W.	Av. T.	Con.	R.	W.	Av. T.	Con.	R.	W.	Av. T.	Con.	R.	W.	Av. T.	Con.	R.	W.	Av. T.	Con.	R.	W.	Av. T.
A	P	4	6		P	5	5	2.4	P	6	4	1.2	P	5	5		P	2	8	5.2	P	5	5	3.7
B	P	4	6		P	5	5	1.8	P	5	5	1.3	P	7	3		P	4	5	.9	P	4	6	2.4
1	1	2	3	49.4	1	2	3	14.2	1	2	3	10.6	1	5	0	16.0	1	2	3	3.2	1	3	2	13.2
2		5	0	54.2		2	3	2.4		2	3	19.2		5	0	11.6		3	2	75.2		2	3	11.2
3		5	0	65.0		2	3	1.6		3	2	21.8		5	0	9.4		5	0	13.8		1	4	5.6
4		5	0	22.2		3	2	1.8		5	0	17.6		5	0	14.8		4	1	2.4		2	3	12.0
5		5	0	19.2		3	2	1.0		3	2	8.8						5	0	13.4		5	0	5.8
6						4	1	4.0		5	0	13.2						4	1	7.0		3	2	5.8
7						4	1	4.4		5	0	5.8						5	0	5.8		3	2	8.8
8						5	0	2.6		5	0	5.0						5	0	10.6		4	1	9.0
9						5	0	2.0		5	0	3.6						5	0	4.2		4	1	8.6
10						5	0	1.6										5	0	5.2		4	1	20.4
11						10	0	1.3														5	0	8.0
12																						5	0	11.0
13														9	1	4.8						4	1	6.6
14														10	0	6.2						5	0	3.6
15														10	0	21.7								
16										10	0	4.2										10	0	1.7
17										10	0	3.5										10	0	3.4
18	2	5	0	33.6	2	4	1	13.4	2	5	0	10.2	2	3	2	229 0	2	3	2	67.0	2	4	1	13.6
19		5	0	9.2		3	2	1.2		2	3	12.4		4	1	145 4		3	2	19.2		3	2	9.8
20		9	1	22.7						8	2	6.0		10	0	29 3						8	2	5.5
21		10	0	11.7						3	7	8.4		9	1	76 7						9	1	9.0
22		9	1	17.8						7	3	13.2		10	0	47 3						10	0	7.8
23										10	0	24.3										9	1	77.8
24	3	4	1	4.0	3	7	3	1.5	3	3	2	28.0	3	5	0	31 6	3	8	2	7.2	3	4	1	16.4
25						5	5	38.2		2	3	32.4						9	1	9.0		5	0	19.2
26	4	5	0	12.0									4	4	1	25 6								
27	6	6	4	7.1									6	4	1	116 0								
28	5	0	5	8.2									5	4	1	60 8								
29	4	5	5	4.7									4	1	1	260 0								

TABLE 7

	No.	Stock No. 81♂			Stock No. 83♂			Inbred No. 87♂			Inbred No. 89♂		
		R.	W.	Av. T.	R.	W.	Av. T.	R.	W.	Av. T.	R.	W.	Av. T.
	A	3	7	2.7	6	4	4.9	1	9	3.1	4	6	.7
	B	6	4	1.1	6	4	12.2	4	6	.7	5	5	.6
1	1	2	3	9.2	3	2	146.8	1	4	17.5	2	3	388.6
	2	4	1	199.5	5	0	65.5	4	1	70.2	4	1	143.8
	3	3	2	73.7	5	0	23.8	4	1	68.9	5	0	82.0
	4	5	0	26.2	5	0	28.7	5	0	68.8	5	0	21.2
	5	5	0	2.2	5	0	9.3	5	0	20.7	5	0	2.3
	6	5	0	1.0	4	1	21.5	5	0	4.1	5	0	2.3
	7	5	0	3.0	5	0	108.7	5	0	14.2	5	0	97.0
2	8	5	0	5.0	5	0	33.5	5	0	7.1	4	1	13.3
	9	5	0	3.1	5	0	23.8	4	1	44.8	5	0	30.5
	10	5	0	3.1	5	0	11.8	5	0	3.9	5	0	34.7
	11	5	0	1.7	5	0	14.2	5	0	1.3	5	0	16.3
3	12	3	2	11.5	5	0	16.3	5	0	3.6	5	0	2.0
	13	4	1	1.9	5	0	26.3	5	0	.8	5	0	3.4
	14	4	1	1.4	5	0	11.6	5	0	1.3	5	0	3.7
	15	5	0	2.2	5	0	7.9	5	0	2.6	5	0	6.0
	16	5	0	1.0	5	0	5.4	5	0	1.8	5	0	1.4
	17	5	0	.8	5	0	2.8	5	0	1.7	5	0	6.1
	18	5	0	2.3	5	0	2.2	5	0	1.7	5	0	1.8
4	19	5	0	2.7	5	0	6.2	5	0	1.0	5	0	5.9
	20	4	1	40.4	5	0	3.1	5	0	13.3	5	0	1.4
	21	5	0	4.2	5	0	2.3	5	0	1.8	5	0	1.3
	22	5	0	3.2	5	0	21.3	4	1	33.1	5	0	5.3
	23	5	0	7.0	5	0	17.2	5	0	31.3	4	1	303.4
	24	5	0	2.9	3	2	181.0	5	0	6.2	5	0	69.9
5	25	5	0	1.6				5	0	41.5	5	0	11.4
	26	5	0	4.8				5	0	10.1	5	0	6.7
	27	4	1	1.1				5	0	10.0	5	0	11.6
	28	5	0	4.2				4	1	7.7	4	1	20.3
	29	5	0	1.7				5	0	14.5	5	0	92.4
	30	5	0	1.2				5	0	6.6	5	0	15.7
6	31	3	2	9.2				4	1	8.0	5	0	.5
	32	3	2	7.3				4	1	12.6	5	0	11.9
	33	4	1	9.0				4	1	10.4	4	1	10.4
	34	5	0	14.7				3	2	19.4	5	0	14.6
	35	4	1	6.9				4	1	91.1	4	1	60.4
9	36	4	1	59.4				5	0	76.5	5	0	3.6
10	37	5	0	47.0				5	0	52.1	5	0	22.9
11	38	5	0	6.4	5	0	273.6	5	0	25.6	5	0	4.4
	39	5	0	20.0	5	0	145.7	5	0	14.2	5	0	8.6
12	1	5	0	77.1	5	0	258.7	5	0	63.3	5	0	21.9
	2	5	0	4.9	5	0	110.0	5	0	38.6	5	0	2.2

TABLE 8

	No.	Stock No. 80 ♀			Stock No. 82 ♀			Inbred No. 84 ♀			Inbred No. 86 ♀		
		R.	W.	Av. T.	R.	W.	Av. T.	R.	W.	Av. T.	R.	W.	Av. T.
	A	4	6	.75	3	7	1.4	4	6	3.9	5	5	1.3
	B	4	6	.66	4	6	4.3	4	6	2.4	3	7	1.6
1	1	3	2	176.4	3	2	112.4	3	2	.6	4	1	1.5
	2	4	1	38.8	4	1	28.2	4	1	49.2	2	3	44.2
	3	5	0	12.3	3	2	11.4	4	1	50.2	5	0	109.6
	4	5	0	16.6	5	0	14.5	5	0	48.5	5	0	127.4
	5	5	0	4.7	5	0	7.4	5	0	37.6	5	0	11.9
	6	5	0	1.5	5	0	2.7	5	0	53.3	5	0	1.9
2	7	5	0	23.7	5	0	3.6	5	0	64.7	5	0	21.3
	8	5	0	6.5	5	0	1.7	5	0	5.6	5	0	8.5
	9	5	0	6.2	3	2	7.6	3	2	70.0	4	1	21.4
	10	5	0	5.8	3	2	67.1	5	0	31.6	5	0	18.2
3	11	5	0	6.9	5	0	108.2	5	0	18.8	5	0	1.4
	12	5	0	7.2	5	0	94.2	5	0	10.8	5	0	18.8
	13	5	0	3.5	5	0	78.2	5	0	7.3	5	0	7.9
	14	5	0	4.6	5	0	20.3	5	0	3.3	5	0	4.9
4	15	5	0	19.5	5	0	16.7	5	0	6.1	5	0	4.1
	16	5	0	9.6	5	0	31.7	5	0	2.8	5	0	3.1
	17	5	0	4.2	5	0	36.5	5	0	3.3	5	0	1.0
	18	5	0	3.7	5	0	21.4	5	0	5.3	5	0	1.0
5	19	5	0	7.9	4	1	23.6	5	0	4.6	5	0	12.6
	20	5	0	40.4	5	0	18.2	5	0	3.1	5	0	2.2
	21	5	0	7.2	5	0	32.8	5	0	10.3	4	1	140.4
6	22	5	0	7.1	5	0	31.1	4	1	3.5	5	0	32.1
	23	5	0	5.6	5	0	20.9	4	1	36.0	5	0	39.3
7	24	4	1	18.1	4	1	11.8	5	0	6.3	5	0	5.8
	25	3	2	66.4	5	0	94.6	5	0	8.7	5	0	1.2
8	26				5	0	16.2	5	0	8.9	5	0	19.6
	27				5	0	14.7	4	1	11.1	4	1	1.9
	28				4	1	30.6	3	2	31.8	5	0	10.0
	29				5	0	38.9	5	0	56.8	5	0	13.5
	30				5	0	39.3	5	0	27.1	5	0	3.3
	31				5	0	99.2	5	0	23.8	5	0	11.0
	32				4	1	25.6	5	0	57.1	5	0	6.8
	33				4	1	81.5	5	0	28.1	5	0	10.2
	34				4	1	104.8	3	2	72.3	5	0	53.0
	35				4	1	105.1				4	1	12.0
	36				5	0	91.9	4	1	10.6	4	1	10.2
	37				5	0	26.1	5	0	36.2	5	0	17.2
9	38	5	0	47.1	5	0	8.1	5	0	34.3	5	0	4.7
	39	5	0	16.9	5	0	13.2	5	0	36.7	5	0	5.5
	1	5	0	15.9	5	0	39.0				5	0	41.7
	2	5	0	1.9	5	0	15.9				5	0	62.4

After the rats had learned to discriminate between the open box and the box covered with black cardboard, a sheet of milk glass was laid over the open box. To increase the difficultness of discrimination thereafter sheets of ordinary typewriter paper were added one by one to the milk glass, cutting off, increasingly, the amount of light entering the light box. The various conditions of discrimination are given thus:

A, B, Preference Series, No Shock

Condition 1. Black cardboard versus open box.
" 2. Black cardboard versus milk glass.
" 3. Black cardboard versus milk glass and 1 paper.
" 4. Black cardboard versus milk glass and 2 papers.
" 5. Black cardboard versus milk glass and 3 papers.
" 6. Black cardboard versus milk glass and 4 papers.
" 7. Black cardboard versus milk glass and 5 papers.
" 8. Black cardboard versus milk glass and 6 papers.
" 9. Black cardboard versus milk glass and 4 papers. Review.
" 10. Black cardboard and paper under, versus milk glass + 4 papers. Review.
" 11. Black cardboard and paper under, versus milk glass. Review.
" 12. Black cardboard and paper under, versus milk glass. Memory.

Table 5 presents the records of the six male rats (stock and inbred); table 6, the six female rats, tested by the earlier workers; tables 7 and 8, similarly, give the records of those tested by the present writer.

In the tables each horizontal black line indicates a change in condition. For conditions 1-5 the rats were required to present perfect records (5 right, 0 wrong) for four successive series of five trials each. Later, when discrimination became more difficult, this was reduced to three, and then to two. When any rat, after making perfect records under the previous easier conditions, began to make one or more mistakes each day, the discrimination was deemed too difficult and the experiment was terminated. When all had reached the limit of their discriminating ability a review series was given to all with only four papers added to the milk glass; then a series of five trials in which a sheet of white paper was laid under the black cardboard to determine whether the rats, by any chance, were choosing because of the difference in the black and white covers rather than by the difference in lightness and darkness.

Finally, after twenty-eight days, two series were given on successive days, as a memory test, under the same conditions as the latest previous test, but with no punishment for failure.

One of the inbred females had died just before these tests were given, but of the seven remaining everyone gave evidence of perfect memory of the habit.

It will be noticed that in the tables for group 1 the records are somewhat irregular owing to the variety of experimenters and to lack of time. It seems worth while to present them, however, as far as they go. The tests under condition 1 were carried out to twenty perfect trials in succession and then in some cases review series were given. The latter are not included in the figures given in table 9. Discrimination under condition 2 with these rats was in no case carried out to the same limit, but it will be noted that even where fifty trials were given, the animals had not succeeded in attaining this standard. It is possible that under these easy conditions of discrimination further training might have ended in perfect discrimination. Observation showed, however, that punishment following repeated errors made the rats both timid and reckless, and the increasing difficulty of working with animals who were frightened, sulky, and careless made it inadvisable to carry discrimination further than condition 3 except in a few trial cases.

The results in these tables present the following facts. (1) There was shown a decided preference by all the rats for the dark box.

PREFERENCE SERIES

		Light	Dark
Group 1	Stock	54	59
	Inbred	52	67
	Total	106	126
Group 2	Stock	36	44
	Inbred	30	50
	Total	66	94

This preference was more marked in the inbred than in the stock rats for the latter of both groups chose the dark 103 times, the former chose it 117 times.

(2) Of the twelve rats of Group 1 only one succeeded in making a perfect record (20 correct trials) under condition 3. Of the four rats which were tested further than this two showed evidence of discrimination under condition 4 but they were not allowed to carry the experiment far enough to secure a perfect

record. All eight of the rats in group 2 (tables 7 and 8) on the other hand, were capable of carrying discrimination as far as condition 6, i.e., cardboard versus milk glass and 4 papers. One stock rat stopped there. The other three stock animals went as far as condition 7, where also one inbred male halted, while the other three were able to discriminate until condition 8 (milk glass and six papers) was reached. The inbred rats therefore were able to discriminate under more difficult conditions than the stock rats.

(3) Two of the stock rats of group 2 after experiencing the electric shock several times under condition 1 made their choices so carefully that only one further error occurred before they reached the limit of their discriminating ability. At that point they were so disturbed by the shocks received that it was impossible to work further with them. Even when the others were ready for the review series they still refused to attempt to discriminate at all. These two rats finished in 24 and 25 series of trials as against 34 and 35 for the others. The average number of trials required to discriminate perfectly under condition 1, condition 2, and the total number of trials (exclusive of review series) given in the discrimination apparatus are shown in table 9.

TABLE 9

AVERAGE NUMBER OF TRIALS IN DISCRIMINATION APPARATUS

	Stock females	Inbred females	Stock males	Inbred males	
Condition 1	41.6	51.6	43.3	76.6	Group 1
	32.5	32.5	30.0	32.5	Group 2
Condition 2	33.3	33.3	30.0	33.3	Group 1
	27.5	32.5	22.5	30.0	Group 2
Totals of all conditions	96.6	102.3	91.6	133.3	Group 1
	150.0	172.5	150.0	175.0	Group 2

From this table it appears that the inbred rats, especially those of group 1, required a larger number of trials under conditions 1 and 2 in order to acquire the habit of discriminating perfectly than did the stock rats. The stock females of group 1 averaged lowest, stock males next, then inbred females and inbred males. Of group 2, the stock males required fewer trials, then the stock females, inbred females and inbred males. Since the inbred continued the experiments under more difficult conditions than the stock rats, it is to be expected that the total number of trials would be greater, but the comparison of figures under conditions 1 and 2 shows that a large part of the total difference is due to differences under the earlier conditions. After the rats had learned to discriminate under the simpler conditions, very few mistakes were made until discrimination became difficult.

The time records (average of 5 trials) of series 1 indicate marked individual differences in the effects of punishment on the different individuals. The two inbred females of group 2 (table 8) made choices very quickly in spite of mistakes and shocks. Their choices were made more slowly on the days following those on which mistakes were made, though never as slowly as were the choices made by some of the other rats. Three of the stock rats and one inbred male were very much delayed in making their decisions by being punished for mistakes. The fourth inbred rat was rendered so excited that after resisting vigorously reentering the apparatus, he dashed wildly in and chose at random, making quick choices and many errors. These facts will be discussed further in the following section.

3. GENERAL BEHAVIOR

In both the maze and the discrimination experiments certain of the differences in behavior of the stock and inbred rats have been indicated in the preceding sections. Notes made each day concerning the general behavior of individuals throw additional light on the differences and help us to interpret them more correctly. To anyone who is accustomed to working with animals nothing is more striking than the fact that no two animals are alike in behavior. Even among white rats the individual peculiarities are so great that the animals can readily be distinguished from one another by behavior alone, by one familiar with their habits.

We will consider first those animals which were tested in both the short maze and the discrimination apparatus, since they form a homogeneous and readily comparable group. From the beginning of the experiments these young rats showed a marked difference in timidity between stock and inbred rats. When the cage door was opened for the stock rats to be removed to the experiment box they would crowd up to the opening, climbing over one another to get out first, running along the edge of the cage and showing no fear of being caught. The inbred rats, on the other hand, after running forward at first, would retreat to the rear corner of the cage and huddle there, trying to escape capture. None of these animals gave any evidence of savageness or wildness.

During the experiments the stock rats paid no attention to occasional noises in the room. The inbred rats, especially in the early experiments, were startled by slight noises and would jump and crouch in a corner.

The stock rats, in the maze experiments, usually ran steadily and rather fast at first, making complex tangles in the outer circles but finding their way to the centre fairly quickly, well within the time limits. They showed much curiosity, poking into blind alleys, stretching to the top of the walls, smelling at the doorways, etc. When acquainted with the maze their speed increased greatly, though here there was considerable variation in method. No. 80, stock female, for instance, ran very fast from the sixth trial on but made very few errors aside from the one of turning in the wrong direction on first entering the maze. No. 82, stock female, on the other hand, ran very fast but in a confused, scatterbrained sort of way, racing back and forth many times in the same alley. Two of the male stock rats ran back and forth repeatedly in the outer circles at first but soon learned merely to look into the blind alleys instead of entering and then ran very fast and quite directly. Only one showed any reluctance to enter the maze and none hesitated to enter the food box.

All the inbred rats, on the contrary, were reluctant to enter the maze; in the first three trials all four ran very little but crouched near the entrance until removed at the end of the time limit. In the fourth and fifth trials they gradually found their way into the centre after lingering near the entrance and wandering in the outer circle. After getting in once each one ran faster, more directly, and soon cut down errors to entering blind alleys once. They showed apparently, therefore, not less ability to form the maze habit than the stock rats but simply a greater timidity in unfamiliar situations, which hindered their forming the habit as quickly. This is borne out by the results of the discrimination experiments where the inbred rats were capable of carrying discrimination further than the stock rats, although they required more time and made more errors in doing so.

An attempt has been made in table 10 to grade these rats in respect to certain characteristics. Since all the animals, when they became accustomed to the surroundings and procedure, would run through the experiments without showing evidences of the timidity and inactivity characteristic of their earlier behavior, the figures given represent the behavior when confronted by new conditions. The characteristics measured are timidity, initiative, sensitiveness, and activity, and the grading is on a scale of 0-5.

TABLE 10

No.,	Timidity	Initiative	Sensitivity to shock	Activity	Maze	Discrimination
Stock						
81♂	1	5	1–2	5	Many errors	Hasty choice. Many errors.
83♂	0–1	4	4	4	Steady, few errors	Careful choice. Few errors.
85♂	0	5	. . .	5	Fast, steady	
80♀	0–1	4	1	5	Fast, few errors	Careful choice. Few errors.
82♀	0	5	1	5	Fast, reckless	Careful, but much running. Excited.
Inbred						
87♂	5	1	3	0	Quiet 2 days	Hard to start. Quick, excited.
89♂	5	3	3	0	Quiet 3 days	Easily excited. When easy, slow, cautious, sure.
84♀	4	4	3	0	Fast	Businesslike.
86♀	5	2	4	0	Quiet 2 days	Careful choice.

On a scale of 0-5, for example, the stock rats showed little or no timidity and great activity; the inbred, on the other hand, just the reverse. Initiative was measured by the readiness with which the rats entered the maze, passed through doorways, or opened by themselves the swing doors of the discrimination box. Sensitiveness was more difficult to measure because of its close relation to timidity. It could not be measured at all in the maze experiments but in the discrimination records those rats were judged not particularly sensitive which rushed back into the dark box immediately after receiving a shock.

In activity, as shown in the discrimination experiments, the rats varied greatly. Some made their choices carefully, with due caution, and with strict attention to business. Others would investigate the box thoroughly, try to climb out, stretch heads into the discrimination chambers, stop to eat, etc After a shock several, especially the inbred rats, would become greatly excited, trying repeatedly to climb over the walls.

In regard to the time taken for each choice the timidity of the animals expressed itself in various ways. The quickest time in which the discrimination could be made was .4″. No. 89, inbred male, made an average for ten trials in preference series A of .7″, and B of .6″. After making two mistakes in training series 1, he was apparently panic-stricken, resisted being urged to enter again, crouched in the alley, darting back to the food box several times. When finally he entered the discrimination chamber he crouched by the door of the dark box, gazing into it without moving for over half an hour. Repeatedly after being shocked he would try frantically to jump out over the edge of the passage. He was large, quick, strong, and active, and when discrimination was easy, made quick trips and quick but careful choices.

The other inbred male (No. 87) showed his timidity in excessive resistance to entering the discrimination box. He would crouch in the passageway in front of the swing doors, and it required much ingenuity and some force to persuade him to enter without getting hurt in the process. Once inside, however, in early experiments, he would dash to one of the boxes, halt abruptly to make a quick comparison with the other, dash in and around to the food box as fast as he could go. All of his choices even when discrimination became difficult, were made quickly but always after careful comparison of the two chambers.

Three of the four inbred rats, even in the preference series where there was no shock to frighten them, were at first too timid to eat when they returned to the food box. One of the females invariably tried to climb out of the small hole in the cover of the food box, a trick none of the others attempted. All four of the stock rats ate readily on returning to the food box, even after having been punished.

In the discrimination experiments one peculiarity was early noticed. Five of the eight rats developed the habit, on entering the space in front of the discrimination chambers, of running immediately to one side or the other, right or left, but always the same for each rat. When discrimination was easy, if that chanced to be the side on which was the light box they would enter at once or stop for a brief comparison of the two boxes. Four of the five always went to the right, one to the left. A sixth one showed a tendency to go first to that side on which the light box had been in the previous trial.

4. ANATOMICAL DATA

Under the conditions of these experiments it was found impossible to have a large number of rats finish at the same time and anatomical data were obtained, therefore, for only the seven rats which survived at the close of the memory tests given after the discrimination experiment. These data are given in table 11.

The section of the table marked W. I. R T. (Wistar Institute Reference Tables) gives data compiled at the Institute, from many rats having the same body length, and serves as a standard for comparison. If we examine the first horizontal line we find that No. 80, stock female, had a body length of 179 mm.; tail length, 144 mm.; body weight 133.5 grms.; brain weight 1.6805 grms.; spinal cord weight .4578 grms.; weight of water in the brain 1.3212; in cord .3296; per cent of water in brain 78.619; in cord, 71.997. Comparing this with the Wistar average of rats having the same body length, we find that in No. 80 the tail length is low, body weight low, brain and cord weights low, and the per cents of water in the brain and cord are high. This is uniformly the case with all seven animals, but it is noticeable that especially in the inbred rats is the per cent of water high. For their age all the rats were under weight, as the Wistar average for males of that age was over 200 grams., and for females nearly 200 grams. It is probable that in feeding the animals only once a day, at the close of the experiments, they did not get enough food for normal growth, although they did keep in good physical condition.

TABLE 11

							W. I. R. T.*				
No.	Sex Age	Body Tail length mm.	Body weight grms.	Brain Cord weight grms.	Weight of water	Per cent of water	Body Tail length mm.	Body weight grms.	Brain Cord weight grms.	Per cent of water	Stock
80	♀	179	133.5	1.6805	1.3212	78.619	.....	144.4	1.754	78.1	b. Apr. 3, 1914—
	173	144		.4578	.3296	71.997	155.7		.508	70.0	d. Sept. 23, 1914
81	♂	191	170.2	1.7391	1.3713	78.851	.....	166.2	1.818	78.1	
	173	151		.5213	.3776	72.434	160.7		.529	70.0	
82	♀	176	136.7	1.5427	1.2178	78.939	.....	136.8	1.740	78.1	
	173	150		.4632	.3355	72.431	152.7		.496	70.0	
83	♂	195	176.8	1.7563	1.3843	78.819	.....	178.1	1.836	78.1	
	173	151		.5528	.3996	72.287	164.5		.545	70.0	
86	♀	177	131.1	1.6283	1.2893	79.181	.....	139.3	1.745	78.1	Inbred
	173	153		.4437	.3229	72.775	153.7		.500	70.0	
87	♂	193	172.0	1.7247	1.3673	79.278	.....	172	1.827	78.1	
	173	162		.5088	.3713	72.976	162.6		.537	70.0	
89	♂	192	167.0	1.7297	1.3689	79.141	.....	169.1	1.822	78.1	
	173	160		.5313	.3890	73.217	161.7		.533	70.0	

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* Wistar Institute Reference Tables.

In order to compare these data with those obtained by Basset[11] in his work on habit formation in albino rats, the averages for these seven rats are given in table 12. Like Basset's rats, these inbred animals have a somewhat greater body-length and body weight than the stock rats, and have a larger per cent of water in the brain and cord. Unlike his rats the brain weight of the inbred rats is greater, not less, so that the relations of brain weight to body length and to body weight are very nearly alike for stock and inbred rats, and very close to Basset's averages for normal animals, a little less in the former case, a bit greater in the latter.

TABLE 12

	Body length in mms.	Body weight in grms.	Brain weight in grms.	Cord weight in grms.	Per cent water in brain
Stock................	185.25	154.3	1.67965	.4987	78.807
Inbred..............	187.33	156.7	1.69423	.4946	79.200

	Per cent water in cord	Per cent brain weight in relation to body weight	Per cent brain weight in relation to body weight	Age
Stock.................	72.287	.90669	1.08856	173
Inbred...............	72.989	.90441	1.08247	173

The data of these experiments differ, therefore, from Basset's in that these rats inbred for thirteen generations did not show a brain weight much less than that of normal rats of an entirely different strain. The results of Basset's experiments showed that his inbred rats of the seventh and eighth generation, having a less than normal brain weight, showed a less than normal ability to form habits, less retention of the habit when formed, and took a longer time to relearn than the normal rats. In the experiments whose results are presented in this paper, a smaller number of animals were tested. Of the rats for which anatomical data were obtained, the inbred learned a trifle more slowly than the stock rats, both in the maze and in the discrimination experiments, but they carried discrimination of lightness and darkness further, and showed the most pronounced difference only in their greater timidity and instability of behavior.

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[11] Bassett, G. C. Habit formation in a strain of albino rats of less than normal brain weight. *Behavior Monographs*, 1914, vol. 2, no. 4, p. 11.

SUMMARY

1. Almost an equal number of stock and inbred rats, because of excessive inactivity, could not be used in the experiments.

2. In the long maze, the male stock rats traveled greater distances, took longer times for the trials, and made more errors, but acquired a perfect habit sooner than the inbred males.

3. In the long maze, the female inbred rats traveled greater distances, took longer times for the trials, and acquired the habit sooner than the stock females. The irregularity in the records is greater. The time records are very high in comparison to distance and errors.

4. When males and females are averaged together, the stock rats show a smaller number of trials required to form a perfect habit than the inbred (55.25 as against 65.00).

5. In the short maze the stock rats acquired the habit sooner than the inbred rats (19.2 as against 23.75).

6. In the short maze the time records are relatively high for the inbred rats, especially during the first few trials.

7. There is greater irregularity in distance and error records for the inbred rats.

8. In the discrimination apparatus all the rats showed a greater preference for the dark than for the light box.

9. The inbred rats showed this preference more markedly than did the stock rats.

10. All the rats learned to discriminate the lighted from the dark box when the difference in illumination was great, and to choose the lighted one in opposition to their preference for the dark one.

11. The inbred rats required a larger number of trials than did the stock rats in order to perfect the habit of choosing the light box.

12. The inbred rats continued to be able to discriminate under more difficult conditions than did the stock rats.

13. The inbred rats showed a brain weight in relation to body length very slightly less than that of the normal rats, and the same is true of the relation of brain weight to body weight.

14. The inbred rats had a larger proportion of water in the brain and cord than did the stock rats.

15. The inbred rats showed an ability to form the same habits as the stock rats but they did it slowly and with greater irregularities from day to day.

16. This slowness seems chiefly to have been due to a greater timidity and a greater susceptibility to environmental conditions.

NOTES ON THE REACTIONS OF BIVALVE MOLLUSKS TO CHANGES IN LIGHT INTENSITY: IMAGE FORMATION IN PECTEN

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Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College. No. 277

Contributions from the Bermuda Biological Station for Research. No. 47

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I. INTRODUCTION

During the summer of 1913, while enjoying the privileges of the Bermuda Biological Station for Research, the writer became interested in the reactions of bivalve mollusks to changes in light intensity. Little more was done, however, than to observe the constancy with which the various species tested responded to shadows, that is, to decreases in the intensity of the light. Further observations were made in the Harvard Zoölogical Laboratory during the first half of the 1913-14 school year, when a few hours each week were devoted to a study of the reactions to changes in light intensity of one of the common fresh-water mussels, Anodonta fluviatilis.[1] I am indebted to Professor G. H. Parker for advice and assistance during this part of the work. Observations on marine forms were renewed the following summer while the writer was occupying a table at the U. S. Fisheries Laboratory at Woods Hole. Here special attention was given to the reactions of Pecten to moving objects.

II. RESULTS WITH ANODONTA

A. Methods

In the experiments on this fresh-water mussel, the following arrangements were made use of for the control of the lights and for making the observations. The vessel in which the animals were placed for experimental study was a rectangular museum jar of a capacity of about 6 liters. Coarse sand was placed in the bottom to a depth of about 5 centimeters, and enough water was added to make a depth of from 10 to 15 centimeters above the sand. The mussels were always placed near one end of the jar with their siphons toward that end, and with their long axes parallel to the longer horizontal axis of the jar. A wooden box was painted black inside and provided with a black cover through which a small observation hole was made. In one end of the box another hole, 5 centimeters in diameter, was bored about 7 centimeters from the bottom, so that its height would correspond to that of the siphons of the mussels when the jar containing them was placed in the box.

Electric lights (incandescent bulbs) were employed as sources of illumination. Two sources were placed on opposite sides of a line which coincided with the long axis of the mussels in the jar and the center of the hole in the end of the box. The lights were so placed that their rays made equal angles with this line. A screen was arranged so that the light from one of the bulbs could be suddenly cut off without interfering with the rays from the other bulb. The screen was not allowed to set up vibrations by touching the floor. Further precautions against vibrations, to which the animals are very sensitive, were taken by supporting the experimentation-box by another box on the cement floor of a basement room, and then placing wads of paper under the lower box, between the two boxes, and under the jar containing the animals. All other light than that used in experimentation was, of course, excluded from the room.

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[1] I am indebted to Mr. W. F. Clapp for advice in the determination of the species mentioned in this paper.

In order to have an expression indicating the intensities of the different lights and their relationships the following formula was employed: Let A equal the intensity of the light—expressed in candle-meters—cut off to produce the decrease; let B equal the intensity of the uninterrupted light—expressed in candle-meters. Then A + B would equal the total intensity before decrease, and $\frac{A}{A + B}$ would be the ratio of the amount of decrease to the total or maximum intensity. For a criterion of equal effects with different intensities, the "inhibition point" was determined; in other words, that value of $\frac{A}{A + B}$ for which A was the lowest intensity at which a response could be obtained when it was cut off. At a slightly lower value for A, B would be great enough, with respect to A, to inhibit a reaction when A was cut off. For the determination of this inhibition point, either A or B could be kept constant and the intensity of the other varied. The value of $\frac{A}{A + B}$ at the inhibition point was used as an index of the degree of sensitivity of an animal.

One source of possible error was the use of the commercial values for the candle-power of the light bulbs employed. The actual intensity of the light falling on the siphons was of course less than this because it had to pass through the glass of the jar and about 2 or 3 centimeters of water. No claim to complete accuracy can be made, therefore, but since the conditions were similar for all the experiments, it is believed that the results are accurate enough to be of value.

B. Results

The points determined in this investigation on Anodonta were, briefly: (1) The degree and kind of sensitivity; (2) the variations in sensitivity among individuals and in the same individual; (3) the recognition of a normal condition of sensitivity, during which could be obtained measurements useful in making comparisons.

1. Kind and Degree of Sensitivity

As a general rule the animals reacted by closing one or both siphons, seldom by closing the valves. The use of greater intensities of light might have resulted in greater muscular contraction in the reactions. The exhalant siphon was far more sensitive than the inhalant siphon and frequently was the only part that reacted to the stimuli. In all the experiments not a single instance was found in which a typical reaction was given in response to an increase in light intensity. On the other hand, decreases so slight as not to be detected by the eye of the experimenter gave rise to unquestionable and typical reactions.

2. Variations in Sensitivity

a. Variations in a Single Individual

The differences in the sensitivity of an animal at different times may be said to be due to differences in the "physiological states" of the animal. In attempting to account for these differences the following factors need to be considered: (1) The previous adaptation to light or darkness; (2) the previous condition with respect to stimulation or non-stimulation; (3) the previous condition with respect to a natural or unnatural position of the body of the animal; (4) the condition of the mantle chamber with respect to the presence or absence of a quantity of foreign material; and (5), probably, the presence or absence of eggs or embryos in the gills of the females.

(1) Only one experiment was carried out to test the differences in sensitivity due to the previous adaptation to light or darkness. In experiment No. 41, mussel No. 203 was left in the experimental box in the dark from 8:15 a. m. until 1:30 p. m., when a series of trials was made in rapid succession to determine the inhibition point. With the light B remaining constantly at a value of 2 candle-meters, the intensity of light A, which was a 10 candle-power bulb, was gradually increased by moving it closer to the animal until it reached the value of 2.5 candle-meters, when a slight but definite reaction was obtained. In this case the value of $\frac{A}{A + B}$ at a point very near to the inhibition point was 0.444. The animal was then left in quiet for half an hour with the lights remaining as above,

that is, A equaling 2.5, and B equaling 2 candle-meters. After this adaptation to a small amount of light, the animal was again tested and barely gave a response when A had the value of 0.5 candle-meters, light B remaining constantly at a value of 2 candle-meters. Under these conditions the value of $\frac{A}{A + B}$ was 0.20. In other words, the sensitivity had increased. This result is just the opposite of that obtained by C. Hess ('10) with Psammobia. He found the ' dark adapted" animals much more sensitive to changes in the intensity of the light than the "light adapted" ones. But in the case of Psammobia the animals were sensitive to increases in light intensity instead of to decreases. In the case of both Psammobia and Anodonta, therefore, the animals became more sensitive after exposure to that condition of their surroundings which tended to be non-stimulating.

(2) During experiments involving successive stimulations with intervals of from one to several minutes, if not carried far enough to cause fatigue, the sensitivity of the animals seems to increase. This was shown in numerous instances, of which the following is a good example. In experiment No. 43, mussel No. 203 was left for 4 hours under a constant light intensity of 10 candle-meters. A few tests showed the value of $\frac{A}{A + B}$ at the inhibition point to be about 0.14, when B had the value of 2 candle-meters. (It is to be noted that the sensitivity in this case is greater than that of the same animal in experiment No. 41, described above, and that the greater sensitivity is correlated with an adaptation to a higher intensity of light.) At the end of 2 hours, during which time half-hour periods of experimentation were alternated with half-hour periods of rest, the sensitivity had risen to such an extent that the value of $\frac{A}{A + B}$ at the inhibition point was 0.04, when B had the value of 2 candle-meters. In view of the 4-hour exposure to a light intensity of 10 candle meters previous to the tests made, it seems most probable that the increase in sensitivity was due to conditions resulting from the stimulations in the subsequent period of 2 hours,

rather than to the possible effect of the two hours additional exposure to light.

The increase in sensitivity in this experiment was of considerable proportions, and its absolute value indicates a rather high degree of sensitivity in these supposedly sluggish animals, for only 4 per cent of the total light intensity needed to be cut off to produce a reaction.

The increase in sensitivity as a result of repeated stimulations is indicated in another way. When an animal is left undisturbed it will spontaneously (i.e., without any observed stimulation) close its siphons from time to time. After a period of stimulation, however, the frequency of the spontaneous contractions of the siphons becomes greatly increased, which increase, it seems reasonable to conclude, is an indication of increased irritability to whatever causes operate to induce such closure when the animals are undisturbed as far as the conditions of the light are concerned.

(3) Occasionally individuals refused to respond in a typical manner, or perhaps refused to respond at all, although at other times the same individuals reacted in a normal way. Since it was noticed that of the various animals taken from the aquarium for experimentation, some were found lying on their sides and others in a natural position, the idea suggested itself that perhaps an unnatural position of the body tended to interfere with normal physiological activities. Such a result would not be unexpected in view of the presence of equilibration organs, in the form of the so-called otoliths. A series of pairs of animals were tested, one member of each pair having been in a natural position, while the other had been lying on its side or on its dorsum for a period of several days. The animal which had been in a natural position reacted in nearly every case more normally than the one which had been in an unnatural position. In a few cases the differences between the members of a pair were not very great, so that some other causes must have been involved in interfering with normal behavior.

(4) At other times, during the course of an experiment, an animal would cease to give consistent reactions. In some of these cases the cause seemed to be the accumulation of foreign material in the mantle cavity. For after a period—usually short—of non-responsiveness, a sudden contraction of muscles

would cause the valves to close partially, and at the same time eject a stream of water from the exhalant siphon carrying with it a greater or less amount of debris from the mantle cavity. Such activities would recur at short intervals until the mantle chamber was apparently free from the foreign material. Then the responses would become normal again. The presence of the foreign material in the mantle chamber seemed to act as a counter irritant, inhibiting for the time being the reactions toward decreases in light intensity.

(5) Some of the largest animals proved to be responsive very slightly or not at all, to decreases in light intensity. They would keep their siphons open wide, with vigorous currents passing in and out of the openings, and fail to close them when the light intensity was reduced. These were gravid females, and their non-responsiveness may have been due to the physiological necessity of maintaining a constant flow of water along the embryo-filled gills.

b. Variations Among Different Animals

The differences in sensitivity among different individuals is perhaps largely to be explained likewise by differences in physiological states induced by the same factors that were found to be effective in single individuals. Doubtless other unrecognized factors are involved in both cases, and individual peculiarities among the clams are also to be expected. A single example will indicate some of the differences to be met with. Mussel No. 203, normally, after stimulation at one-minute intervals for 15 or 20 minutes, begins to show irregularities in the responses, doubtless due to fatigue, and these irregularities increase if the stimulation is continued. In one experiment mussels Nos. 203 and 205 were placed side by side and subjected to the same conditions. No. 203 failed to open its siphons at all on this occasion, while No. 205, on the other hand, reacted to decreases in light intensity promptly and without any irregularities every minute for 50 minutes, at the end of which time the experiment was discontinued.

3. Comparative Measurements of Sensitivity

A sufficient number of experiments were performed on mussel No. 203 to make it possible to recognize a normal type of behavior for this individual. When it was responding normally, values of $\frac{A}{A + B}$ could be obtained which were comparable. This line of experimentation was not pursued very far, but some examples of the results obtained will be given. In one series of experiments (Nos. 42-46) conducted on different days, a number of tests were made in the course of each experiment. When the value of light B was allowed to remain constantly at 2 candle-meters, and the value of A varied till the inhibition point was reached, the values of $\frac{A}{A + B}$ were successively, for the different experiments, 0.14, 0.14, 0.10, 0.14, and 0.125, which show a fairly close degree of correspondence. In experiments Nos. 44-46, further tests were made with higher intensities of light. In these additional tests, the value of light A remained constantly at 22.2 candle-meters and the value of B was varied till the inhibition point was found. In these cases the value of $\frac{A}{A + B}$ at the inhibition point were successively 0.078, 0.08, 0.08, which series also shows close agreement. But the sensitivity in the latter case is seen to be very much greater than in the former. This increase may have been due to an increase in sensitivity accompanying the use of higher intensities of light, as was indicated on page 301, or to an increase in sensitivity due to previous stimulation (for the values for the higher intensities were obtained after those of the lower intensities) or to both causes. This line of experimentation, if pursued further, would permit the testing out the applicability of the Weber-Fechner law to the behavior of these animals.

The results obtained from these few experiments on the fresh-water mussel, while incomplete and fragmentary, nevertheless may indicate some lines of experimentation which might profitably be pursued further.

III. RESULTS WITH MARINE SPECIES

The experiments and results at Woods Hole may be grouped under two heads: (A) qualitative tests with different species, and (B) results with Pecten.

A. *Qualitative Tests with Different Species*

1. Classification Based on Sensitivity

Nagel ('94) has called the sense by which animals distinguish changes in light intensity "der photoskioptischen Sinn," or light-shadow sense, and speaks of animals as being "photoptic" or "skioptic," when they are sensitive respectively to increases or to decreases in light intensity. He gives a list of over 20 species of bivalves that he has tested and divides them into 6 classes, grading from purely skioptic through photoskioptic to purely photoptic. I find it more convenient to group the species tested at Woods Hole into 3 classes, viz.:

a. Sensitive both to increases and decreases.

1. Mya arenaria
2. Ensis directus
3. Venus mercenaria
4. Petricola dactylus
5. Spisula solidissima
6. Callocardia morrhuma

b. Sensitive to decrease only.

1. Pecten gibbus (var. borealis)
2. Ostrea virginiana
3. Modiola demissus (var. plicatula)
4. Modiola modiolus
5. Mytilus edulis
6. Liocardium mortoni
7. Anomia simplex (?)

c. Sensitive neither to increases nor decreases

1. Cumingia tellinoides
2. Yoldia limatula
3. Solenomya velum
4. Tellina tenera
5. Nucula proxima (?)

A question mark is placed after Nucula because the animal is so small and the siphons so short that slight movements may have been overlooked. So far as could be observed, however, there were no reactions. Since Nagel ('94) puts Tellina complanata and T. nitida rather high in the photoskioptic class, it may be that my failure to get responses from T. tenera was due to unfavorable physiological states of the animals experimented with. There is also some question about the position of Anomia simplex, for, although the animals tested reacted only to decreases, it is probable that the change from a depth of 8 to 10 meters—the level at which they were collected—to the surface caused a very great decrease in physiological tone. Such a loss in physiological tone was especially noticeable in Pecten and Arca collected from similar depths. In fact, Arca failed to give any consistent responses. I failed to find any species which reacted to increases only. Some of those in class *a* reacted more strongly to increases than to decreases, e.g., Venus, but all except those in class *c* reacted to decreases.

2. Relation of Sensitivity to Presence or Absence of Pigment

It is worthy of note that all the species named in classes *a* and *b* had more or less pigment deposited on the ends of the siphons, or along the edge of the mantle, as in Pecten and Ostrea; and these pigmented areas seemed in every case to be the parts sensitive to changes in the intensity of the light. In class *c* there was a total lack of pigment so far as I could discover by examining the living specimens. The correlation of the presence of pigment with the sensitive areas of these animals is in accordance with a general rule throughout the animal kingdom. That pigment is not necessary to such sensitivity has been well established by Beer ('01), R. Hesse ('02), and others. Nagel ('96) finds that Psammobia has no pigment on the siphons, yet it is very sensitive to increases in light intensity. On the other hand, I have found that Cummingia, which has relatively very long, non-pigmented, separate siphons, that move about actively, gave no sign of sensitivity to either increase or decrease in intensity in any of the two or three dozen animals that I tested. While the correlation between the presence of pigment and sensitivity is apparently perfect as far as my investigations go, this is not proof but that species may be found on our eastern coast for which this correlation fails to hold.

3. Differences in Reactions to Increase and Decrease of Light Intensity

Another point may be noted with respect to some members of class *a*, namely, that in certain cases, and especially in that of Mya, a different set of muscles is involved in the reaction to increase from that involved in the reaction to decrease of light intensity. Time after time specimens of Mya were tested and the reactions followed the same general rule, viz., for decreases in intensity, the movement was that of the muscles involved in closing the siphonal openings, while in responses to increases, the siphon tubes were withdrawn. In the latter case the withdrawal of the siphon tubes was sometimes accompanied by closure of the openings, especially if the reaction was a vigorous one, but as a general rule, when the movement of the siphon tube was not great, no closure of the openings resulted. Just why one set of muscles should be used for the reaction to increases and another set for reactions to decreases, is difficult to understand. Since Mya usually inhabits stretches of the shore which are exposed at low tide, it might be thought to be an adaptation to the conditions of its habitat for the siphons to be withdrawn as the tide goes out, accompanied as it would be with gradual increases in light intensity. But under the conditions of the experiments the reaction was to a sudden increase in the intensity of the light rather than to a slow or gradual increase. Another possibility is that the reaction is due to an increase in heat rather than to an increase in light. Experiments were not undertaken to determine this point. On the other hand, it is equally difficult to understand why decreases in intensity, which might accompany the approach of an enemy, were responded to by a mere closure of the siphonal openings, without a withdrawal of the siphon tube. A similar difference in reaction was noticed in Petricola and Spisula.

B. Results with Pecten

1. Sensitivity to Increase and Decrease

It will be noticed that Pecten is placed in class *b*, that is, among those which react to decrease only. Nagel ('94) classes Pecten and Arca among those which are "photoskioptic," but Dakin ('09) and Bauer ('12) say that Pecten does not react to increases in intensity. It is not strictly correct to say that Pecten does not react to increases, for at times sudden increases, especially when the light is very strong, will cause the animals to close their valves. But such reactions are very irregular and occur only after a latent period of several seconds (Nagel mentions the long latent period for reactions to increases). On the other hand, the reaction to decreases is nearly always immediate and regular. With respect to immediate and regular responses, therefore, it is proper to place Pecten gibbus (var. borealis) in class *b*. This property of Pecten seemed to offer an oppotunity to test the image-forming powers of its eyes by employing a moving object in such a way that it would be accompanied by an increase instead of a decrease in the intensity of the light.

a. Methods

For these experiments the following methods were employed. In a wooden box, about 45 x 30 x 30 centimeters, a hole about

4 centimeters in diameter was bored at one end near enough to the bottom to correspond to the height of the animals when they were placed in a dish containing sand and the dish was set in the box. On the outside of the box a circular disk of bristol board, blackened with India ink, was fastened at its center so that it could be rotated. Openings of various sizes were made in the disk near its periphery in such positions that they would coincide with the hole in the box when the disk was rotated. In a rough way, therefore, the amount of light falling on a given area of an animal could be controlled. For cutting off the light a separate black card was passed between the box and the light source (usually the window) close to the box but not touching it. Further precautions were taken to prevent vibrations, to which many species are very sensitive, by supporting the box and the dishes containing the animals on wads of cotton.

b. Results

Under the above conditions it was found that Pecten was very sensitive to decreases in light intensity, but reacted seldom to increases, and then only after a relatively long latent period. There was therefore little danger of confusing the two types of reactions. It was further observed that Pecten reacted more readily to decreases when the illumination was low, than when it was very bright. Low intensity corresponds more nearly to the conditions of their natural habitat than does high intensity, and it may be that their greater sensitivity at the lower intensities is an adaptation to their normal surroundings. Pecten differs in this respect from Anodonta, which lives in much shallower water.

Rawitz ('88) stated that a considerable number of eyes must be affected by a shadow in order to produce a response. Some attempts were therefore made to limit illumination to a small area of the mantle margin. By means of narrow slits or small round openings in the disk, it was possible to restrict the area subjected to bright illumination. In these cases direct sunlight was reflected from a mirror. In one instance only two eyes were thus illuminated, yet definite reactions followed the cutting off of the light. In several instances of this kind, where only a small area of the mantle edge of one side was illuminated, the response to a cutting off of the light was a very local muscular contraction involving little more than the illuminated area. These results are certainly quite different from those reported by Rawitz. Dakin ('10*a*) also states that a considerable number of eyes must be affected by a shadow in order to produce a reaction. Rawitz and Dakin, however, used small objects to produce local shadows instead of the local illumination method just described. The difference in method may account for the different results. The local responses obtained as a result of localised stimuli indicate their reflex character.

2. Reactions Toward a Moving Object

a. Experiments

For testing the image-forming powers of the eye in Pecten, the following methods were employed. A piece of bristol-board about 25 x 15 centimeters was blackened with India ink and pasted to a piece of heavy cardboard to give it rigidity. This was used as a background for the moving object, which was a white card 7.5 centimeters square. The animals were placed in the end of the box bearing the hole and the revolving disk, and the black bristol-board was stood up in the opposite end, that farthest from the window. To the white card a black thread was attached and passed vertically over a convenient gas jet—in lieu of a pulley—so that the card could be raised and lowered without the corresponding movement of the hand being visible to the animals.

First the animals were tested for increases and decreases in the usual way. Additional tests for increases were frequently made by flashing on to the animals a reflection of the light from the window by means of a mirror held in the hand. If the animals were found to be reacting normally, they were then tested with the moving card. Since the white card was receiving the light from the window, it will readily be understood that as the card moved upward from the bottom of the box, it would receive more and more light, and therefore would reflect more and more light on to the Pectens in the other end of the box. Each upward movement of the card would therefore be accompanied by an increase in the intensity of the light to which the animals were subjected. Any reaction they might give, therefore, could not be attributed to a decrease in the intensity of the light. Nevertheless, whenever the card was moved upward the animals gave immediate and vigorous responses by closing the valves or by contraction movements of the vela and tentacles. The reactions followed alike when the movement of the card was slow—i.e., about 5 centimeters per second—or when the card was suddenly jerked upward. Similar reactions were also obtained when the card was moved downward, or from side to side at a constant level. When a black card was substituted for a white one, reactions sometimes resulted, sometimes not. I cannot be certain whether there was enough contrast in the amount of light reflected from the background, compared to that from the card, to allow the animals to form an image of the moving black card, or whether some slight movement of the arm or body of the observer in connection with the pulling of the thread may not have been the source of the stimulus. That the eyes were concerned in the reception of the stimuli from the moving cards is indicated by the results of the following experiment. In all the previous experiments the animals were always placed with the open, or ventral, side toward the moving card. Now they were turned around 180 degrees so that their dorsal, or hinge, side was toward the card. In this position light from the card could not fall on the eyes and the animals gave no responses to the movement. Next they were turned back 90 degrees, so that either the anterior or posterior margins with their eyes were turned toward the card. In this position they gave fully as vigorous responses as when the ventral side was toward the card.

In one series of experiments the size of the white card was successively reduced to determine the lower limit of size to which the animals would respond. The smallest card, the movement of which produced a definite reaction, was 1.5 centimeters square and its distance from the animal about 35 centimeters. No attempt was made to determine a larger limit, nor any distance limits.

It is believed by the writer that these experiments with the upward moving white card on a black background, since any possibility of the movement being accompanied by a diminution of the intensity of the light was excluded, and since definite and vigorous responses were obtained, constitute a demonstration of the ability of the Pecten eye to form an image. Perhaps absolute proof could only be obtained by removing all the eyes and then subjecting the animals to the same tests. Such a method might also demonstrate whether the eyes alone, or other parts of the mantle-border as well, are sensitive to the changes in light intensity. But the operation involved would undoubtedly be a great shock to the animals and their subsequent behavior might not be typical.

b. Discussion

The complex and highly organized structure of the eyes of Pecten has attracted the attention of histologists for many years. Those who have undertaken a careful study of the structure have usually found many difficulties to overcome, and unsatisfactory results were often obtained on account of imperfect technique. The most recent, and perhaps the most reliable, detailed study of the Pecten eye is that of Dakin ('10*b*), to which the reader is referred.

Many of those who have studied the histology of these eyes have assumed that the animals could "see" with them. The following quotation from Garner ('37) indicates the typical attitude among some of the earlier investigators: Garner says (p. 488): "In Pecten, Spondylus, and Ostrea we find small, brilliant, emerald-like ocelli, which, from their structure, having each a minute nerve, a pupil, a pigmentum, a striated body, and a lens, and from their situation at the edge of the mantle, where alone such organs could be useful, and also placed, as in Gasteropoda, with the tentacles, must be organs of vision." Similarly, on anatomical grounds, Grube ('40), Rawitz ('88), Schreiner ('97), R. Hesse ('00), and others conclude that these eyes are organs of vision. But very few of the histologists have performed crucial experiments to determine whether or not Pecten really could form an image. And some of them have indulged in various speculations as to some function other than vision.

As an example of such speculations I may quote Hickson ('80). He says (p. 454): "Little is known and little can be said concerning the function of the eyes of Pecten. The presence of such a well-formed tapetum makes it probable that they are capable of appreciating very diffused light. The close approximation of the lens to the retina makes it exceedingly improbable that any image is formed upon the latter. A few experiments have been made on the extent of their visual power, which make it very doubtful whether they are of much value to the animal in avoiding its enemies. The most reasonable theory of their function seems to be that, when on the ebbing tide a probability arises that they will be left high and dry on the shore, they can appreciate the fact by the growing intensity of the light, and by the peculiar flapping motion of their valves the Pectens are so remarkable for, move away into deeper water."

Sharp ('87) criticises this idea of Hickson, calling attention to the well-formed eyes of the species found in the Mediterranean, where scarcely any tide exists. Earlier ('84), he had said (p. 458): " Now, I am inclined to believe, as has been suggested by Hensen ('65), that the pigmented epithelial cells that cover this organ and the stalk on which it is situated, and the only place where we find a marked deposit of pigment, is the seat of vision for these animals and that the so-called eye may be an organ of some other sense. . . . If the organ in question is so highly developed, we must necessarily conclude that vision, if that be the sense, is also highly developed, which does not appear to be the case. . . ." But in 1886 he offers the suggestion that they are phosphorescent organs, saying (p. 61): " It is not unreasonable to suppose that organs for emission of light would be constructed on the same principles as those for the admission of light." Dakin ('10*b*) tested out this phosphorescent theory and obtained only negative results.

Patten ('86) regarded the eyes of Pecten and Arca as organs for the absorption of energy from the sun, and termed them "heliophags." This idea has received no support from later investigators.

Attention should be called to the fact that Pectens, as well as other bivalves, fail to give consistent responses unless they are in good physiological condition. I found this to be true of all the different species experimented with, and in the case of Pecten I was able to get consistent responses only from those collected in very shallow water. Animals collected from a depth of 10 to 12 meters gave irregular responses and usually died at the end of two to four days in the laboratory aquaria.

As already stated, Rawitz ('88) claimed that no reactions were obtained from Pecten unless the shadow furnishing the stimulus affected several eyes, i.e., a considerable length of mantle edge. The shadow of a small object, such as a needle, brought no responses unless the shadow was made to fall on a series of eyes in quick succession, in which case the stimulation was the same as if a larger object had been used. From these results, and from the study of the structure of the eye, he concluded that the animals possessed a mosaic type of vision, saying (p. 548):

" Wird somit in jedem Auge nur ein kleiner Teil desjenigen Objectes abgebildet, welches sich gerade im Gesichtsfelde befindet, und sind zur deutlichen Wahrnehmung immer eine grossere Zahl von Augen notwendig (wie viel, weiss ich nicht; doch ist die Zahl der notwendigen Augen für diese Batrachtung nebensächlich), so heisst das· das Gesamtbild, welches eine Muschel wharnimmt, setzt sich aus einer bald grosseren, bald geringeren Zahl von Einzelbildchen zusammen, die linear aneinandergereiht sind. Wir haben es hier also mit einer Art musivischen Sehens, und zwar linearen musivischen Sehens zu thun." Rawitz made use of shadows in his experiments, thereby failing to make a distinction between reactions to decreases in the intensity of the light and reactions to the movement of an object. It would have been possible to have attributed the reactions he obtained to decreases in light intensity alone. As previously stated, I obtained responses with decreases when only two eyes were illuminated. Unfortunately, I did not attempt to determine the reaction of a single eye to the moving card in my experiments.

Nagel ('94) distinguishes between the sensitivity to changes of light intensity, which he called the "photoskioptic sense," and the sensitivity to the movement of an object. He says (p. 387): " Im Gegensatz dazu (photoskioptic animals) würden die ikonoptischen Tiere solche sein, bei welchen zu den photoskioptischen Wahrnehmungen der einzelnen sensiblen Elemente die Perception eines durch einen lichtbrechenden Apparat erzeugten Bildes hinzukommt." He regarded Pecten as "ikonoptic" and says ('96, p. 64): " Die verscheidenen Arten von Pecten, welche bekanntlich Augen in erheblichen Zahl am Mantelrande tragen, schliessen ihre Schalen schon, wenn man nur in the Nähe kommt, ohne dass ein Schatten auf sie gefallen wäre." While this latter statement is probably correct, these reactions might have been the result of very slight decreases in illumination due to the approach of the observer, or his passage between the animal and some of the windows of the room. I have obtained similar results under similar circumstances but regarded the observations as far less conclusive than those made in connection with the experiments with the moving card.

Greater conservatism is shown by some of the investigators, who have not jumped to unproved conclusions. Drew ('06, p. 50) says: "It is difficult to determine how well a scallop sees. . . . Quick motions outside of an aquarium made so the illumination is not materially affected and so the aquarium is not jarred, frequently seem to cause responses, but the results are so frequently negative that apparent responses may be accidental. Experiments to test the power of vision have not been devised." Differences in physiological states may account for the inconsistent results obtained by Drew.

Dakin ('10*b*) experimented on various kinds of Pecten and states (p. 102): "The eyes show no evidence of being phosphorescent organs, though I have observed and stimulated them at night and in the dark. A shadow thrown on to the eyes of an open Pecten causes a closure of the valves, and this reaction usually takes place very rapidly, though very often the perception of light stimuli does not appear to be any better than by Arca with very simple eyes or others with pigment spots." Dakin further states that no evidence of accommodation could be obtained experimentally. In regard to pigment spots it may be worth while to mention that the Pectens used in my experiments possessed, in addition to the eyes, pigment spots along the mantle edge similar to those found on the mantles of eyeless forms, and these pigment spots may be sensitive to changes in light intensity. However, the only method of testing the matter seems to be that of eliminating all the eyes and then subjecting the animals to changes of light intensity.

Only a few investigators have carried out careful experiments to determine the extent of the powers of vision in Pecten, and usually no adequate discrimination has been made between reactions to decreases in light intensity and the possible reactions to the movement of an object. Bauer and von Uexküll have performed the most critical experiments on Pecten. Bauer ('12, p. 134) says: "Es muss dagegen betont werden dass bei Pecten nicht die Harebsetzung der Lichtintensität den auslösenden Reiz darstellt, sondern dass das Tier die Bewegung des Schattens 'sieht'." In support of this conclusion he points out that when an opaque object is passed between the animal and the light source, there may be obtained an upper and a lower limit of rapidity with which the object can be moved and still produce a reaction. But in this experiment no distinction is made between the effect of the movement and that of a diminution of the light intensity. However, he relates that in preparing his camera for photographing the animals in the aquarium, the movement of his arm before the dark background of the black-cloth camera-cover was sufficient stimulus to cause a reaction. There was no shadow in this case, according to his statement. He also performed a series of experiments to determine the rôle of the eyes in the righting reflex (" Umkehrreflex") and concludes that they are vitally concerned in, and necessary for, the carrying out of this reflex.

Von Uexküll ('12) got the usual results with a shadow, i.e., closing of the shell. When, however, he placed a starfish—a natural enemy—on the glass side of an aquarium adjacent to the one in which the Pectens were confined, there was not the response that was to have been expected if the Pecten "saw" its enemy. The starfish was then made to move and the Pecten responded by extending its tentacles in the direction of the starfish. Dakin ('10*a*) showed that when fluid drawn from a chopped-up starfish was pipetted on to the tentacles of a Pecten it would close its shell or swim away. Von Uexküll argues, therefore, that a series of reactions is involved in the closure of the shell following a stimulation of the eyes by a moving object. The perception of the movement causes a positive reaction of the tentacles which extend toward the moving object. If the tentacles then receive a stimulation by some chemical substance, the shell is closed by the adductor muscles. In my experiments with the moving card there was no intermediate reaction of the tentacles, the reactions to the movement of the card being in nearly every case an immediate closure or partial closure of the valves. In the case of Von Uexkull's experiment, however, there seems to be no reason to doubt that the animals did react to the movement of the starfish, thus indicating the ability to form an image.

Thus while some experimental evidence has been produced indicating an image-forming capacity for the eyes of Pecten, many of the experiments have been uncritical in that they have not been conducted so as to distinguish between reactions to decreases in light intensity and reactions to the movement of an object. The experiments and observations of Nagel, Bauer, and Von Uexküll, however, seem to be fairly conclusive. It is believed that the experiments described in the present paper were so conducted as to avoid any confusion of the two kinds of stimulation, and therefore, to establish that Pecten gibbus (var. borealis) responds to the movement of an object and consequently may be thought to form an image in its highly organized eyes.

IV. SUMMARY

A. Results on Anodonta: 1. Anodonta is sensitive to decreases in light intensity but not to increases. Responses were obtained to decreases so slight as not to be detected by the eye of the observer

2. Sensitivity is influenced by the physiological states of the animals in at least the following ways: (a) Animals kept in the dark a few hours are less sensitive than when kept in the light, even when the light is very weak (e.g , 4 or 5 candlemeters). (b) Animals are more sensitive after periods during which successive experimental stimulations were given than after periods of quiet. (c) Unnatural positions of repose for the animals seem to interfere with normal sensitivity. (d) The presence of foreign material in the mantle chamber may temporarily inhibit reactions to stimulation by decreases in light intensity. (e) The presence of eggs or embryos in the gills of gravid females appears to inhibit responses to decreases in the intensity of the light. (f) Inherent differences in sensitivity between individuals probably exists.

3. By letting A equal the amount of light (expressed in candlemeters) cut off to produce a decrease, and B equal the amount of uninterrupted light (expressed in candle-meters), the degree of sensitivity may be measured by the value of the fraction $\frac{A}{A + B}$ when A has the lowest value for which a response is given.

B. Results on marine species: 1. Three classes were distinguishable as follows: (a) Those sensitive to both increase and decrease in light intensity (e.g., Mya); (b) those sensitive to decrease only (e.g., Pecten); and (c) those sensitive neither to decreases nor to increases (e.g., Cumingia).

2. A perfect correlation was found for the animals studied, between sensitivity and the presence of pigment in the epithelium of the sensitive areas.

3. In the case of Mya arenaria, and some others, reaction to increases resulted in a withdrawal of the siphon tubes, while reaction to decreases resulted in a closure of siphonal openings, often unaccompanied by any withdrawal of the tube.

4. Experiments on Pecten, which is sensitive only to decreases (with exceptions noted in the text), demonstrated that: (a) vigorous reactions by closing the valves may be obtained when a white card is moved over a black background, even when the movement involves an increase in the intensity of the light falling on the animals. This is believed to show that the Pecten eye may form an image. (b) The smallest white card the movement of which produced a response at a distance of 35 centimeters was 15 millimeters square. (c) When bright illumination was employed reactions occurred on decrease in intensity even if only two eyes were affected. Response in this case was local.

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NOTES

NOTE ON THE BEHAVIOR OF CAPONS WHEN BROODING CHICKS

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References to the brooding of chicks by capons are often found in the literature but descriptions of their behavior do not seem to be on record. During the past season five tests with capons have been made. Two of the capons used were Rhode Island Reds, a race in which the females are very much inclined to broodiness and make excellent mothers, while three were Brown Leghorns, a race the females of which rarely become broody. The chicks used have all been Rhode Island Reds. They readily accept the capon as a foster-parent. Much of the success of the experiments is due to the excellent care given the birds by the foreman of the poultry yards, Mr. John Sayer.

First instance.—This capon was a Rhode Island Red hatched in April, 1913, and caponized in late July in the usual commercial manner by an expert caponizer. He had all the usual characteristics of his kind. The chicks were four in number, hen-hatched and also brooded by the hen for the first two or three days of their lives. The capon was placed in a coop on the night of May 20, 1914, and two of the chicks placed beneath him. He accepted them without trouble and hovered them from the start. The remainder of the chicks were given to him the next morning. During the day he was taken a little distance from the coop, leaving the chicks behind. On being released, he returned at once to his charges. The capon and his flock were then removed from the coop and given the run of a large yard. The chicks followed the capon about, who clucked to them occasionally in an *imperfect* way as though he did not quite know how to do it, and found bits of food for them. Although somewhat disturbed when approached, he did not ruffle up his feathers and spread his wings as a hen would do, but simply retreated. Neither did he cluck as often nor as regularly as a hen.

By this time it was evident that the chicks would be cared for by the capon and the brood accordingly was removed to an out-door yard. The capon showed no disposition to leave his charges, though adult birds, including his recent companions, were in neighboring yards. In a few days the cluck of the capon became more like that of a hen, the bird giving voice to it frequently as he walked about the yard. He continuously hunted food for the chicks and on finding a morsel called the chicks to it as a hen would do, but less vociferously. He also attacked anyone who attempted to interfere with the chicks but did not give a call like the warning call of the hen as far as observed. When these chicks were about three weeks old, another lot of chicks a week younger was added to the flock. The capon accepted these without trouble, though confined in a relatively large yard, 18 x 50 feet. Hens do not as a rule accept chicks much younger than their own. The new chicks, however, were somewhat slow to follow their foster-parent, partly because they were weaker. It was necessary on this account to round up the flock once or twice the first day. The next few days were uneventful, but before the new chicks were a week old a hen in an adjoining yard came off with two ducklings. About one-half the younger chicks promptly deserted the capon and adopted the hen.

Thus far the behavior of the capon, as far as caring for the chicks is concerned, has been essentially like a hen. There are, however, two points in which he differed decidedly from hens. First, the capon began caring for the chicks without becoming broody or without previous training. The chicks were simply placed beneath him and he began to care for them. The hen becomes first broody, i.e., stops laying, remains continuously on the nest, clucks and ruffles her feathers when disturbed, and sometimes, at least, will not take chicks until she has been broody for some time. The second point was wholly unexpected and adds to the general anomaly of the capon's behavior.

This point of behavior may be described as follows: At one moment the capon is moving sedately about. Suddenly he seizes one of the chicks by the nape of the neck and dangling it in the air squats and goes through sidewise shaking movements of the posterior part of the body, as a cock does when treading a hen. The orgasm is soon over; the struggling chick is released and the capon resumes his rôle of caretaker. Sometimes, though not often, the act is repeated two or three times with the same or different chicks within a short time—ten or fifteen minutes. On one or two such occasions, I have seen him employ a trick used by the cock in getting a hen indifferent to his attentions within reach. This trick consists in uttering the food call, at the same time standing with head down, repeatedly pretending to pick up and drop an imaginary bit of food, but at the same time with an eye on the hen. When she comes within reach, he attempts to seize her. A hen with chicks calls them to the food but in a different way. The capon's behavior toward the chicks leaves little room for doubt that he is attempting to tread them. Though hens have since been kept in the same pen, this capon has not been observed treading them. This capon reared all the chicks given him.

In the second instance the capon was a Brown Leghorn, hatched June 29, 1913, and caponized by the writer August 8, 1913. The same procedure was adopted with the Brown Leghorn as with the Rhode Island Red. The hen-hatched chicks were accepted just as readily as before. However, he was extremely wild, so that whenever anyone approached he promptly attempted to escape from the coop or yard in which he was confined. He made no attempt to fight off an intruder but promptly deserted his charges for the far corner of the pen. As soon, however, as the intruder withdrew he returned to the chicks. This bird clucked very little, even when he had a tidbit to offer. His movements were very quick. After a little he learned to fly out of the pen, and as the meshes of the wire were coarse, the chicks were able to follow him. Only two of the four originally given him survived beyond the first few days. The trio kept together all summer until the capon moulted. Soon after his new feathers were about two-thirds grown he was observed at several different times on top of a post, crowing. In appearance he is as typical a capon as any other.

The third instance was a Rhode Island Red capon of similar history to the first. The chicks used were incubator-hatched. The bird was shut up in the evening of July 12 and two chicks placed beneath him. He took them readily. The following night the rest of the hatch, some twenty-five in number, was placed beneath him. The entire flock was accepted and cared for. This bird from the start clucked more like a hen than the first capon used. The chicks and capon were kept in a loft for a few days, and then placed in a large "A" coop out-of-doors, the chicks being allowed to run out between the slats. This capon took most excellent care of the chicks. He was never observed making any attempt to tread them.

The fourth capon was a Brown Leghorn of similar history to the others. He was given incubator-hatched chicks in early September. They were poor chicks and died after a few days. This capon was fairly quiet and as far as could be seen gave the chicks good care while they lived, which was less than a week. Before the bird's band number was taken, a heavy wind blew open the door of the coop, permitting his escape. He returned of his own accord to the pen which contained the flock of capons, so that it is uncertain whether this or another Leghorn was used in the fifth trial.

Much the same procedure was employed in the fifth trial as with number four. The capon, a Brown Leghorn, was placed in a coop in a loft and given five chicks, three of which soon died. A few days later he was removed out-of-doors into a large "A" coop. This bird, while somewhat wild at first, soon quieted down and paid little attention to people who came near the coop. He wandered up and down the coop very much like a hen, with an eye on the chicks which ran at large. His cluck, made at intervals, sounded much like that of a hen. The chicks spent most of the time racing about outside the coop. As far as observed he did not attempt to tread the chicks. If released from his coop he led the chicks about like a hen, scratched for them and called them to him. If one picked up a chick, the bird spread himself like a hen and advanced to the attack.

The general behavior of capons is anomalous. In many respects quieter than normal males, they do not as a rule give evidence of sexuality. Usually, they impress one as being essentially neutral in sexual behavior, very much like any immature bird. Darwin states that they are said to incubate eggs as well as care for the chicks. We have not yet tested this report. Their behavior with chicks, in the main, is very much like that of the hen, such differences, with the exception of the actions of the first capon in treading the chicks, being of a minor character and difficult to distinguish clearly from those of a broody hen. On the other hand they sometimes crow and may give attention to the hens, their behavior at such times being as complex as that of the cock.

It is remarkable that the Leghorn capons should receive the chicks quite as readily as the Rhode Island Reds. Since the females rarely become broody (only two or three per cent) one would not expect to find such strong evidences of the broody instinct in capons of this race. The differences in the races with regard to broodiness is well marked. Of the Reds, only about two per cent *fail* to become broody at least once during the first year, while many individuals become broody eight or ten times within a year from the time they begin to lay. We have no statistics of our own on the Leghorns, but a breeder of white Leghorns reports that his records show that of nearly three hundred pullets only twelve became broody (most of them only once) but one became broody five times and one three times. My own experience with Brown Leghorns is of the same general character. As a rule, Leghorns that show signs of broodiness rarely make good mothers, for the exhibitions of broodiness are very transitory.

Although the tests are not extensive enough to warrant definite conclusions, it would appear possible that the brooding instincts of the capon are after all not necessarily a female character. Many male birds, e.g., pigeons, assist in brooding and rearing the young. The domestic cock sometimes assists the hen in finding a nest. An instance of a broody cock which hatched a clutch of eggs was recently published in "Fur and Feathers." Darwin states in "Animals and Plants," as follows: "The capon takes to sitting on eggs, and will bring up chickens. . . . Reaumur asserts that a cock, by being long confined in solitude and darkness, can be taught to take charge of young chickens; he then utters a peculiar cry, and retains during his whole life this newly acquired maternal instinct."

Tests of non-broody hens, castrated hens, normal males and chicks of various ages from various races will have to be made in order to throw more light on the question of the capon's behavior. Older chicks are sometimes used as leaders in teaching very young chicks the way in and out of a brooder. A single test that was made of a normal male gave negative results.

Obviously, until more studies have been made of the behavior of fowls, the brooding instinct of the capon cannot be cited as proof of the assumption of a female secondary sexual character by a castrated male.

NOTE.—In a recent paper in this journal Pearl makes the following statement: "It appears to be the case that in the domestic fowl the brooding instinct has to a large degree disappeared along with the fact of domestication." He points out that at the Maine Station they have found great difficulty in finding hens that would incubate eggs through the full period of twenty-one days. My own experience with several varieties of poultry, extending over several years, does not coincide at all with Pearl's. Instances in which the birds fail to complete the full period have not been frequent. At various times, by providing a fresh lot of eggs, hens have been made to incubate eggs for six weeks or longer. In the Little Compton district, a noted poultry center, hens are depended upon almost entirely for hatching and rearing chicks. The natural method is also used extensively by farmers and poultrymen in general. The interesting results reported by Pearl would seem to apply only to *some* flocks of birds belonging to the so-called broody races (Rocks, Wyandottes, Orpingtons, etc.), but can hardly be considered of general applicability to such races. Quite the reverse, however, would be true of the Leghorns and similar non-broody races where, as stated above, only a small per cent show any traces of the broody instinct.

THE HABITS IN OVIPOSITION OF THE BEETLE *BRUCHUS*

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Beetles belonging to the genus *Bruchus* may either deposit their eggs upon the outside of the young pods of large-seeded legumes (*Phaseolus*, *Pisum*, *Vigna*, *Vicia* and others) through which the young larvae penetrate to the developing seed, or upon the surface of the dry, stored seed.

If the behavior[1] of the insect in oviposition be dependent in any degree upon the characteristics of the young pod, such modification of behavior as may take place because of the varying characteristics of the developing ovary may (although it will not necessarily) be recorded in the differences in the incidence of parasites as determined from samples of matured seeds drawn from pods of known matured characteristics. One cannot assert upon failure to find a relationship between the characteristics of matured pods and the incidence of parasites that some such relationship does not exist in the case of the young pods. On the other hand, a relationship actually demonstrated on the basis of matured pods only should be interpreted with caution. These statements are true for the reason that the degree of agreement between the characteristics of mature and developing pods is not fully enough known. It is here that direct observations upon behavior seem almost indispensable.

The analysis of the data[2] for two experiments, involving quite dissimilar horticultural varieties and comprising 6,233 and 8,018 pods maturing 18,575 and 21,231 seeds respectively, leads to the following conclusions for *Phaseolus*:

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[1] These dates were secured in connection with some physiological work on seed weight in beans in which it became necessary to consider the question of the incidence of *Bruchus o-tectus* in experimental cultures of *Phaseolus* made several years ago. They are presented in full in the *Journal of the New York Entomological Society*, December, 1915. The purpose of this note is to call the attention of students of animal behavior to an addition to the list of instances in which records made by the organism itself may greatly facilitate the study of behavior, and to the need for direct observations upon behavior supplementing the data here given.

[2] The seeds studied were parasitized almost exclusively by insects developing from eggs on the pods in the field. I cannot assert that *none* were parasitized in storage, but if an appreciable number were so injured it makes the results here given even more significant, since any random injury would tend to obscure differential parasitization.

1. No relationship between the position which a seed occupies in the pod and its liability to parasitization has as yet been demonstrated.

2. The relative number of seeds which are parasitized[3] increases from pods with the lower to pods with the higher numbers of ovules. That is to say, the percentage frequency of seeds which are injured by parasites is higher in pods with the larger numbers of ovules. Of course this percentage is based upon the total number of seeds matured, not upon the total number of ovules[4] originally laid down.

3. The same relationship holds for the number of seeds matured per pod and the incidence of the parasites. The seeds are relatively more extensively infested in pods maturing larger numbers of seeds.

4. It is difficult to differentiate and to measure the independent influence[5] of these two characters of the ovary upon the incidence of the insects. Apparently the number of seeds matured has some influence independent of that of the number of ovules per pod with which it is correlated. Since this relationship seems to be slight, it is probable that the number of ovules laid down is the primary factor.

The simplest hypothesis in explanation of the observed relationships would seem to be that in the young pods size is correlated with the number of ovules formed and the number of seeds which are beginning to develop, just as they are known to be in matured pods of other forms,[6] and that in consequence the maintenance of a foothold and oviposition are easier in the larger ovaries. This is, however, merely a suggested hypothesis which must be confirmed or disproved by actual behavior studies.

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[3] In any future studies of this kind the seeds should be so preserved that the number of insects, if more than one, which emerge from each seed may be determined.

[4] The number of ovules per pod includes the number of seeds actually matured and the number of abortive seeds.

[5] Since number of seeds matured and number of ovules formed per pod are positively correlated (Harris, J. Arthur, *Arch. f. Entwicklungsmech. d. Organism*, **35**, 500-522, 1912) a relationship between either of these characters and the incidence of weevils would necessarily result in some relationship between the other character and frequency of parasitization, even though there were no direct causal relationship between them.

[6] Harris, J. Arthur, *Bot. Gaz.*, **50**, 117-127, 1910; *loc. cit.*, **53**, 204-218, 396-414, 1912.

TONE AND NOISE PERCEPTION IN THE WHITE RAT

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In the field of human psychology, studies in audition seem gradually to be accumulating evidence in favor of a resonance theory of perception. In a previous paper I have pointed out briefly some of this evidence.[1] It has been shown by Ewald that a thin rubber membrane nearly as small in its dimensions as the human basilar membrane can be made to take up sympathetically the vibrations of a tone. In this experiment the membrane was suspended in a liquid as is the basilar membrane. It seems highly probable at present that either the basilar membrane or some other structure in the cochlea can serve as a resonator of a low degree of elasticity, and can respond sympathetically to periodic vibrations and to vibrations that do not depart far from periodicity. That different parts of this resonating structure respond to tones of different frequencies is an hypothesis that gets support directly and indirectly from various kinds of facts, some of which have been suggested in the paper mentioned above. Resonators in the ear, however, do not necessarily imply specific energy of the nerve elements in the cochlea, and *vice versa*.

Evidence for or against the specific energy theory of hearing has frequently been derived from experiments upon animals, coupled with the destruction of certain parts of their cochleas. In the paper to which reference has been made I pointed out the fact that Kalisher's results, now well known, were not to be relied upon. The experiments of Johnson[2] have completely disproved the validity of Kalisher's conclusions. Johnson's experiments, as well as those by Hunter,[3] make the evidence both for and against the specific energy theory, obtained by destruction of sections of the cochlea, practically worthless, even to those who had overlooked the obvious imperfections of such experiments as they had been carried out. With improvement in methods of determining reactions to specific sounds, however, the problem may be attacked with some degree of success; but there still remain grave difficulties in connection with the operative technique.

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[1] The place of stimulation in the cochlea versus frequency as a direct determiner of pitch, *Psychol. Rev.*, XX, 1913, 312ff. Cf. Hardesty, *Am. Jr. Anat.*, **18**, 471ff.

[2] Audition and habit formation in the dog, *Behavior Monographs*, **2**, no. 3, 1912.

[3] The auditory sensitivity of the white rat, *Jour. An. Behavior*, **4**, 1914, 215-222. and **5**, 1915, 312-329.

Yerkes found that the dancing mouse is deaf to all sounds, except for a few days early in life.[4] The examinations of the cochlea of this animal by such investigators as Rawitz, Cyon, Alexander and Kreidl, and Kishi are not very satisfactory from a number of standpoints. For example, the fitness of structures in the cochlea for resonance of tones, a difficult matter to determine, is a question that is not answered. The recent experiments of Hunter, checked by various controls, seem to indicate that the rat is deaf to tones in the lower end of the scale—possibly to all tones—while it hears noises of the same predominant pitches. Hunter suggests that if after all "there is a sensitivity to tonal stimuli as here tested, then, for the rat, tones and noises are very different classes of stimuli."[5] Miss Barber, working under Hunter's supervision, has found similar evidence for the rat's deafness to tones,[6] and has suggested[7] that her own and Hunter's results, indicating a sensitivity to noises and an insensitivity to tones, "may point to separate bases for the perception of noise and tone." What may be the nature of these bases is not conjectured. It is on this point that I wish to make a suggestion.

If Hunter's results prove to be correct, the white rat should furnish us valuable data toward settling the question as to how the ear analyzes the complex vibrations of the air waves; for there can be little doubt that tone perception by the ear follows the same principle in the higher animals as in man. Why the rat fails to hear tones and yet hears noises should be discoverable somehow, and the answer will likely require careful anatomical as well as experimental work.

Personally I do not believe that in animals just above the rat in hearing—animals hearing both noises and tones—separate structures are involved in noise and in tone perception. To explain Hunter's results, in case they prove to be correct, we need only posit a lack in the rat's ear of suitable structures for resonance, thus making possible only forced, or highly inelastic, movement of cells in the cochlea. The basilar membrane may consist of tissue, for instance, too loose and flabby for resonance; or there may be ossification under the basilar membrane, as has been found by Shambaugh to be the case under the narrower end of the basilar membrane of the pig's ear. Various other conditions may be responsible for the lack of sympathetic resonance in the white rat's cochlea, but it is useless to speculate on them further. It is sufficient, in our present ignorance of the real nature of the rat's cochlea, merely to set the hypothesis so as to direct the attention of anatomists to matters which are crucial and which have not infrequently been overlooked in anatomical investigations.

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[4] The dancing mouse, 1907, 52-92.
[5] *Op. cit.*, vol. V, 327.
[6] The localization of sound in the white rat, *Jour. An. Behavior*, **5**, 1915, 292-311.
[7] *Ibid.*, 311.

If there are no structures in the white rat's ear suitable to serve as resonators periodic vibrations will have very slight stimulating effect. Noises coming with richer and more irregular pulsations would therefore be audible even though tones are inaudible. It would be interesting to try periodic vibrations of very low frequencies, near man's lower limit. The intensity of all tones should be as great as possible. Miss Barber used as a control an interrupted organ pipe without, I believe, giving the period of interruption. Further experiments along this line with various frequencies, both of the interrupted tones and of the interruptions themselves, might give significant results The periods of interruption should doubtless be below the frequency of the lower audible limit. Noises of a slightly different kind from those used might be produced by the irregular striking of the keys of the piano or organ. Can the rat be made to respond to such " noises "?

Even the results already obtained on the white rat, indicating certainly considerable difference in the perception of noises and of tones, will present difficulties of no small importance to non-resonance theories of hearing.

A CUBAN CHIMPANZEE[1]

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Translated from the Spanish by C. S. Rossy[2]

In a notable report on " The order of the Primates: an anatomical parallel between man and apes " (Paris, 1877), Broca, in discussing the phenomena of gestation and the evolution of certain parts of the foetal membranes in the Primates, states that in this connection one can say very little about the anthropoid apes, because these animals do not reproduce themselves in captivity, and that " the little that is known of them has been observed from some female killed while in gestation." For this reason, the procreation and birth of a chimpanzee in Cuba constitutes a scientific event worthy of registration in the annals of natural science. According to our knowledge, it is the first time that an anthropoid ape has been born in captivity. The following data have been obtained concerning the family of the anthropoid ape to which we refer.

Jimmy, the father, came from London to Havana in 1914. This adult chimpanzee, 11 to 12 years of age, measures in height 1 meter and 13 centimeters. He is irascible and wild.

Cucusa, the mother, an adult chimpanzee from Sierra Leona, 12 to 14 years of age, is a beautiful specimen of anthropoid ape. She measures 1 meter and 30 centimeters, and her thoracic perimeter reaches 90 centimeters. Cucusa had previously indulged in amorous relations with Chimpí, a chimpanzee which lived in the park of the "Quinta Palatino," the estate of Dona Sra. Rosalia Abreu, from 1904 to 1914. He was a notable anthropoid on account of his intelligence. Because of certain intimate abnormalities of his physical constitution, Chimpí had no succession. He died at the age of 14 years as the result of acute myelitis, according to the reliable data revealed at an autopsy made by Dr. Raimundo Menocal.

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[1] A paper read before the Cuban Society of Natural History, " Felipe Poey," on October 30, 1915.

[2] In this translation a few paragraphs which lacked scientific value have been omitted. The original article was published by *El Siglo* XX, Havana.

Lastly, the young chimpanzee, product of the relations between Jimmy and Cucusa, was baptized with the name of Anumá (a Simian divinity of India). It was born on the 27th of April, 1915, a date from now on memorable in the calendar of births of anthropoid apes.

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About Jimmy I have very little to say, except in reference to the original posture that this ape takes in the act of reproduction. It is known that even in their most intimate acts the apes show the least possible modesty; and, due to this peculiarity, observers have been able to be present during the act of generation, *coram populo*, and to witness the classic position, *more canum*, in this interesting species of animals. Jimmy, however, presents an exception to this classic position. When this master and lord of the cage experiences ardent desires of possession (and this happens very frequently), he sits on the floor, stretches his legs out close to each other, and strikes the floor with the dorsal side of the hands, the fingers relaxed. This signal must be well known to the female, because, whenever she is surprised by it, she turns her head and, without the slightest vacillation, very passively comes to the male, who is waiting in the posture already described. Then she turns her back to him and sits on his thighs, opening her legs at the same time that she executes a movement of inclination towards Jimmy's feet,—prostrating herself, in other words, in the attitude of a Mussulman praying. During the act, the female remains passive until the end, the male assuming all the active part of the function.

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With regard to Cucusa, pregnancy was first suspected in the month of August, 1914, because, at the catamenial period, the genital turgency was moderated while there was also a decrease in the flow of blood. These symptoms were significant, as it is known that at these periods the development of the external genital parts reaches a voluminous size. During this period also, Cucusa's usual joviality disappeared; at the same time, she was losing appetite, showing a certain dislike for food, which was expressed sometimes in actual vomiting.

Soon there could be no doubt as to her true condition, as the mammary glands were becoming more prominent and the abdomen was showing already a sensible volume; furthermore, all signs of catamenia disappeared during the last three months of pregnancy.

This last fact definitely settles the doubt expressed by Broca in his report on the order of the Primates: "Regarding the anthropoids, the question of the catamenial flow has remained doubtful up to the present time, as there has been no occasion to study female adults in captivity." Cucusa, in her normal condition, sometimes has had very abundant losses of blood. Another fact which should be mentioned, being of interest to naturalists, is that, contrary to what is observed in the case of most mammals, sexual relations between Jimmy and Cucusa continued during the whole period of gestation, both day and night.

Finally, nine months after the first visible symptoms were observed, Cucusa gave birth to Anumá on the 27th of April, 1915. This event established the duration of gestation of the anthropoids, which up to the present has been unknown, although suspected to be approximately as long as we have indicated.

The parturition of the anthropoid ape must have taken place between 5 and 6 o'clock in the morning, as at 6 o'clock the young ape was first noticed, resting on the contracted legs of the mother and still joined to her by the umbilical cord. His body was completely hairless, with the exception of the head, on which hair was abundant. His eyes were wide open and his gaze indicated bewilderment.

The attitude of the mother at the moment of birth escaped observation. Nevertheless, everything has led us to believe that the obstetric posture of Cucusa was a crouching position, as is the case among other apes.

At 7 o'clock in the morning the umbilical cord appeared separated from the mother, but still adherent to the umbilicus of the young chimpanzee. No one assisted in the severing of the umbilical cord. The placental extremity, together with pieces of the membrane and two clots of blood, was found on the mattress on which the mother was lying. In one of these clots, the eminent histologist of the faculty of medicine, Dr. Valentín Castanedo, discovered a placental cotyledon, which was shown in the preparation presented to the "Sociedad Poey." It is regrettable that we have not been able to obtain the placenta in this case, as very little is known concerning the placentae of the anthropoid apes.

(The author here quotes a statement from Madame Louise Toussaint[3] regarding the custom among apes of eating part of the placenta after parturition, and then severing the umbilical cord.)

Bouchacourt[4] emphasizes the fact that all animals after parturition eat their placentae, just as the birds eat the shells of the eggs after the hatching of the young.

We are, therefore, led to believe that Cucusa ate the placenta, as all other apes (monkeys) have done which have given birth to young in the park of the "Quinta Palatino."

During the first two days after parturition, Cucusa, somewhat fatigued, often lay down on her back. She lost very little blood. From the third day, she could easily climb to the board which was fastened high above her bed and which served as a resting place. Lactation began on the second day. Sixteen days after birth, that is, on the 13th of May, there was a normal return of catamenia with an abundant flow for twenty-four hours, but without external genital turgency.

The umbilical cord, dry and flattened, continued to adhere to Anumá for approximately thirty-six hours after birth. We took care to preserve it and find that it measures 70 centimeters. Through the examination of Dr. V. Castanedo we have learned that it contains the normal human constituents.

When Anumá was two months old four incisors appeared, two in the upper jaw and two in the lower jaw. During the third month the remaining incisors developed and, during the fourth month, four molars followed.

Anumá is at present six months old and measures in height 53 centimeters. The circumference of the head is 33 centimeters and the thoracic perimeter is 37 centimeters.

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[3] Toussaint, Louise. Causeries d'une accoucheuse. Paris, 1910.

[4] Carnot, Dr. Paul. Opoterapia. Paris, 1911.

THE REFRACTIVE POWER OF LENS AND FLUID MEDIA OF THE MAMMALIAN EYE

STELLA B. VINCENT

In the paper on the mammalian eye in this Journal, vol. 2, p. 249, there are errors in the figures for the refractive indices. Mr. H. M. Johnson has kindly called my attention to this and I am very glad to give the corrections. The figures for the lens were omitted from the table and the confusion is caused by misplaced headings. The refractive figures for the horse have been shifted to the raccoon and this is also true of the description of the sensitive area of horse in column three. For fear that there might be other errors I have carefully verified all the factual material in the tables from the original articles. The figures below as they should have appeared in the original table are taken from Gustav Freytag, Die Brechungsindices der Linse und flussigen Augenmedien bei Katze und bei Kainichen, *Arch. f. verg. Opth.*, 1910, Vol. 1.

	Refractive Index Aqueous Humor	Refractive Index Vitreous Humor	Refractive Index Lens
Ape....................	1.33322	1.3338	1.4245 (Matthiessen)
Cat....................	1.33009	1.33006	1.4465 (11 mos.) 1.4514 (7 yrs.)
Dog....................	1.3349	1.33483	1.4498 (1.25 yrs.) 1.4666 (15 yrs.)
Horse..................	1.33378	1.3338	1.4338 (10-12 mos.) 1.4484 (22 yrs.)
Rabbit.................	1.33069	1.33045	1.4174 (9 days) 1.4652 (5.50 yrs.)